

A Confluence of Sturgeon Migration: Adult Abundance and Juvenile Survival

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**Abstract**

This dissertation provides new information crucial to the recovery and management of Green Sturgeon (*Acipenser medirostris*). First, we present a novel method to estimate Green Sturgeon abundance using DIDSON acoustic cameras. This method outperformed traditional capture-recapture methods in measures of precision, effort and disturbance to the target species. We then implemented this method to develop estimates of run-size and population size for the Southern Distinct Population Segment of Green Sturgeon. Finally, we developed an individual based model that tracks the growth and survival of juvenile Green Sturgeon during the first 45 days of their outmigration. We found that water temperature had the greatest influence on total biomass produced while migration rate had a lesser effect on produced biomass. We then determined that Green Sturgeon still have access to the most productive regions of their spawning habitat using this model to evaluate produced biomass across time and space.

# Estimating the Riverine Abundance of Green Sturgeon Using a DIDSON Acoustic Camera

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## <A>Abstract

To determine the total number of Green Sturgeon *Acipenser medirostris* present in the Rogue River, Oregon, we compared plot sampling using a DIDSON acoustic camera, a density based estimation technique combining the number of individuals detected and the area sampled, to a concurrent mark-recapture estimate. Using the DIDSON-based method, we estimated the total abundance of Green Sturgeon to be 223 (95% confidence interval = 180 - 266). The mark-recapture method resulted in an estimate of 236 (150 - 424). The non-invasive DIDSON transect estimates resulted in tighter confidence intervals and required fewer technician hours to collect the data (37 vs. 232 hrs). Precise estimates of the abundance and distribution of Green Sturgeon are important components to species recovery and management. Thus, this new technique has the potential to greatly improve population monitoring and is an excellent tool to identify occupied habitats.

## <A>Introduction

Many terrestrial and aquatic genera are imperiled, and freshwater fish species are among the most at risk (Ricciardi and Rasmussen 1999). Sturgeons are considered some of the most at risk freshwater species, and Billard and Lecointre (2001) listed overfishing, habitat degradation and pollution as the primary causes. Currently, six species in the United States are listed under the Endangered Species Act (Adams et al. 2007). The Green Sturgeon (*Acipenser medirostris*) is an anadromous species that spawns in three rivers along the west coast of the United States. The species is composed of two populations, the Northern Distinct Population Segment (NDPS) which spawns in the Rogue and Klamath River systems, and the Southern Distinct Population Segment (SDPS) which spawns in the Sacramento River system (Adams et al. 2007, Seesholtz et al. 2014). The SDPS is listed as a Threatened Species by the U.S. Endangered Species Act (NMFS 2006). Currently, the size and demographic composition of Green Sturgeon populations are unknown.

Previously, no direct methods have been used to monitor population size or total number of adult Green Sturgeon. In a status assessment, Adams et al. (2007) reviewed available indices of Green Sturgeon abundance and found that inconsistent sampling and estimation methods led to biases that impaired the author's ability to assess population sizes. These indices resulted from the harvest by Yurok tribe in the Klamath River, assessments of White Sturgeon by California Fish and Wildlife in the San Francisco Bay, and entrainment within a major water diversion in the California Central Valley. Israel and May (2010) provided a novel application to estimate SDPS breeding population size using larvae sampled downstream of spawning sites. Unfortunately sampling from their study occurred in the upper portion of the known SDPS spawning range,

omitting breeders in the lower reaches. All of these methods result in an incomplete estimate of the breeding population size. Thus, the evaluation of these two population's status requires a monitoring method applicable throughout the species entire range.

Studies on the distribution of Green Sturgeon have traditionally relied upon the capturing and handling of individuals. Early investigators of the spatial distribution of Green Sturgeon analyzed the returns of external tags recaptured by fisherman (Miller 1972) or the detection of eggs and larvae to infer habitat usage (Kohlhorst 1976). These types of studies can provide insights into the geographical distributions of entire populations, but suffer from small sample sizes that reduce the precision of these estimates. This problem has been circumvented by implementing acoustic tags and a spatially diverse network of passive tag detecting hydrophones to understand spawning migrations (Erickson and Webb 2007; Heublein et al. 2008), estuarine distribution (Lindley et al. 2011) and habitat preferences in the near shore and riverine environments (Mora et al. 2009; Huff et al. 2011). Habitat use in the open ocean has also been provided by pop-off satellite archival tag and trawl bycatch data (Erickson and Hightower 2007). The addition of actively tracking individuals has greatly informed understanding of fine scale distribution and individual movement (Erickson et al. 2002; Benson et al. 2006; Thomas et al. 2014).

We present a rapid and non-invasive method to assess adult Green Sturgeon abundance during their spawning period using a Dual Frequency Identification Sonar (DIDSON, Sound Metrics, Bellevue, Washington). Applications of DIDSONs in fisheries research have varied from assessments of abundance and distribution (Becker et al. 2011), escapement (Holmes et al. 2006;

Pipal et al. 2010) and evaluations of sturgeon behavior (Crossman et al. 2011). To introduce this method we present a comparison of a DIDSON-based transect estimation technique with a mark-recapture estimation technique based on multiple gill-net sampling events. Our study had two objectives. First, we compared the accuracy and precision of the two abundance estimation methods. Second, we compared the number of technician hours required in the field to gather data for the two methods.

### **<A>Methods**

The Rogue River is a major river along the West Coast of the United States, draining approximately 13,000 km<sup>2</sup> of south western Oregon. Our study was conducted in the lower 73 kilometers during October 2007 (Figure 1). Average river discharge during this period was 70 cms as measured at the USGS gaging station near Agness (USGS Station 14372300). In the Rogue River, Green Sturgeon are able to access the lower 118 rkm up to Raine Falls and are generally found in reaches greater than 5 m deep (Erickson *et al.* 2002). Our depth surveys identified 65 reaches or “habitat units” satisfying this criterion. In these habitat units we performed presence-absence surveys using DIDSON and subsequent abundance estimates by performing DIDSON transects as well as gill-net sampling when sturgeon were identified as present.

A DIDSON operates similarly to a medical ultrasound apparatus, emitting high frequency sound and compiling the returns into an image in real time. This occurs several times per second, thus the resulting data creates a movie-like image of ensonified objects. We were able to distinguish substrate types (sand, sand waves, cobble and boulders), smaller fish in the water column, trees



and other objects. Sturgeons are large bottom oriented fish and are easily differentiated from other fishes in the DIDSON record due to their large size, benthic orientation and swimming style (supplemental video). DIDSON has a measure too to determine the size of objects, thus calibrating the scale of what is viewed. By pausing playback of the files and measuring objects on screen we were able to use size (approximately 2 m in length vs. 1 m salmonids) as a criterion to identify sturgeon. Additionally, as the distance between the ensonified fish and its acoustic shadow is short (<1 m) the object is bottom oriented. There are no other fish genera in the Rogue River that display these two characteristics. DIDSON has two modes of operation, high frequency and low frequency. The high frequency mode ensonifies a smaller area but images are clearer and show more detail than the low frequency mode. During low frequency mode the DIDSON is able to view a larger area (approximately 15 m in width when water depth is near 7 m) but at a sacrifice to image clarity. We operated DIDSON in low frequency mode because the larger sampled area was preferable for detecting sturgeon presence and to calculate their densities. We mounted the DIDSON to the gunwale of a jet boat using a custom manufactured pan and tilt mount modified from Enzenhofer and Cronkite (2005).

**<B>Presence absence surveys.** —

At each of the 65 habitat units, we sampled for the presence of sturgeon using DIDSON. At each unit, we performed a minimum of three transects with the DIDSON focused toward the bottom of the river, forward of the survey vessel. In this orientation the beam width was 29 degrees oriented shore to shore and the beam height was 14 degrees oriented top to bottom. Viewing window length was set to 20 m and the window start was varied between 5 and 15 m depending on depth. During each transect, the survey vessel drove longitudinally through the entire length of the habitat unit, either upstream or downstream, while personnel viewed DIDSON images in

real time. If sturgeon presence was confirmed, we estimated the number of sturgeon present using the two methods described below. If sturgeon were absent, we moved to and surveyed the next unit.

**<B>DIDSON abundance estimation. —**

When sturgeons were present in a habitat unit, we used a plot sampling abundance estimator to estimate the number of sturgeon present. We performed between 3 -7 transects and recorded unique DIDSON files for each transect. Transect paths were collected using a GEO XT GPS (Trimble, Sunnyvale, California). We viewed each DIDSON file three times and tallied the number of detected sturgeon in each file. When two counts were the same for a file, that number of detections was judged the number of detected sturgeon. The average of the three counts was used if three counts disagreed. Transect widths were calculated from the DIDSON files using the measure tool in DIDSON software as sampled width varies with depth as well as DIDSON angle from horizontal. We measured the width of the DIDSON beam where it intersected the river bed at the 25<sup>th</sup>, 50<sup>th</sup> and 75<sup>th</sup> percentile frames of each transect and calculated the mean to represent the transect width. The sampled area for each transect was calculated in ArcGIS (ESRI, Redlands, California) using a buffer around each transect path with half the calculated transect width representing the buffer distance. The total sampled area per unit was calculated in ArcGIS as the minimum convex polygon containing the buffered transects.

We estimated the number of sturgeon present at each habitat unit and the total number of detected sturgeon using the following equations:

EQ(1) 
$$\hat{D}_i = \frac{\bar{y}}{a}$$

where  $\widehat{D}_i$  is the estimated sturgeon density at habitat unit  $i$ ,  $\bar{y}$  is mean number of sturgeon detected per transect and  $\bar{a}$  is the mean sampled area per transect. The total number of sturgeon at unit  $i$  was estimated as:

$$\text{EQ(2)} \quad \widehat{Y}_i = A_i \widehat{D}_i$$

Where  $\widehat{Y}_i$  is the estimated number of sturgeon at unit  $i$ , and  $A_i$  is the total sampled area at unit  $i$ . An estimated variance of the estimated mean density of sturgeon at unit  $i$  from transects  $j_{1-n}$  is calculated using the area-weighted least-squares variance estimator introduced here:

$$\text{EQ(3)} \quad \widehat{V}(\widehat{D}_i) = \frac{\frac{1}{n} \sum (\frac{a_j}{\bar{a}})^2 (\widehat{D}_j - \widehat{D}_i)^2}{n - 1}$$

An estimated variance of the estimated total number of sturgeon at unit  $i$  is:

$$\text{EQ(4)} \quad \widehat{V}(\widehat{Y}_i) = A_i^2 \widehat{V}(\widehat{D}_i)$$

An estimate of the total number of sturgeon detected during the sample period is:

$$\text{EQ(5)} \quad \widehat{T} = \sum_i^n \widehat{Y}_i$$

An estimated variance of the estimated total number of sturgeon detected during the sample period is:

$$\text{EQ(6)} \quad \hat{V}(\hat{T}) = \sum_i^n \hat{V}(\hat{Y}_i)$$

Confidence intervals for the within-unit totals were calculated as:

$$\text{EQ(7)} \quad CI_i = \hat{Y}_i \pm \sqrt{\hat{V}(\hat{Y}_i)} t_{(\alpha/2),n-1}$$

where  $t_{\alpha/2}$  is the entry in a one-sided t-distribution table for the desired alpha and  $n$  is the number of transects performed at habitat unit  $i$ . Ninety five percent confidence intervals for the total number of detected sturgeon during the sample period were calculated as:

$$\text{EQ(8)} \quad CI_{Total} = \hat{T} \pm \sqrt{\hat{V}(\hat{T})} t_{(\alpha/2),n-1}$$

White Sturgeon (*Acipenser transmontanus*) is present in our study area and indistinguishable from Green Sturgeon using DIDSON. We estimated the proportion of detected sturgeon that were Green Sturgeon ( $P$ ) from our captured records as the ratio of captured Green Sturgeon ( $C_G$ ) to the total number of captured sturgeon ( $N_c$ ):

$$\text{EQ(9)} \quad \hat{P} = \frac{C_G}{N_c},$$

which can be approximated as a binomial proportion with mean  $\hat{P}$  and variance:

$$\text{EQ(10)} \quad \hat{V}(\hat{P}) = \frac{\hat{P}(1-\hat{P})}{N_c}$$

We estimated the total number of detected Green Sturgeon ( $\widehat{T}_G$ ) as:

$$\text{EQ(11)} \quad \widehat{T}_G = \widehat{P}\widehat{T}$$

To estimate the variance of  $\widehat{T}_G$  we used a form of the Delta Method applicable to two independent random variables (Seber 1982):

$$\text{EQ(12)} \quad V[\widehat{T}_G] = (\widehat{P})^2 \widehat{V}[\widehat{T}] + (\widehat{T})^2 \widehat{V}[\widehat{P}] + \widehat{V}(\widehat{P})\widehat{V}(\widehat{T}).$$

Confidence intervals for the total number of detected Green Sturgeon were calculated as:

$$\text{EQ(13)} \quad CI_{\widehat{T}_G} = \widehat{T}_G \pm \sqrt{\widehat{V}(\widehat{T}_G)} z_{(\alpha/2)}.$$

The DIDSON-based estimation method makes five assumptions:

- 1) A closed population. No sturgeon emigrates or immigrates during the surveys.
- 2) 100% detection. If a sturgeon is in the view of the DIDSON, then it is detected and tallied.
- 3) The calculated densities are unbiased. Thus, measurements of transect area and number of sturgeon detected are unbiased.
- 4) All locations where sturgeon are present are surveyed. No aggregating sites are omitted from the survey.

- 5) All sturgeon are in the sampled units. No sturgeon are in transit between units during the survey.

To evaluate how sturgeon densities and number of transects influence the bias and precision of this estimation method we performed sampling simulations using the R package WiSP (Zucchini et al. 2007). At three uniform distributions of  $N=5, 25$  and  $50$ , we simulated 100 site visits consisting of 20 randomly placed transects per site visit in a  $125\text{ m} \times 300\text{ m}$  habitat unit.

Transects ran parallel the entire length of the habitat unit similar to the field transects. Transect widths were set at 10 m wide. For each site visit we calculated two metrics. First, we calculated the running estimate after each transect using equation (1). Second, we calculated the running coefficient of variation (CV) of the estimate of the total using the ratio of the square root of equation (4) to equation (2).

***<B>Mark Recapture Estimate.*** —

We also estimated the abundance of sturgeon using gill nets in order to verify the DIDSON-based estimate(s). We deployed two  $3.0\text{ m} \times 30\text{ m}$  20 cm stretch gill-nets at habitat units where sturgeons were identified as present from DIDSON sampling. These nets were fished for one hour each with 30 minutes between settings for a total of three sets per habitat unit per day. We sampled in each unit for three days with one day rest between site visits resulting in nine sets per habitat unit. Captured sturgeons were marked through the base of the dorsal fin with a loop ended spaghetti tag inscribed with a unique five digit numerical ID, implanted with a passive integrated transponder (PIT) tag, and released to the habitat unit where captured.

We analyzed the resulting data with closed-population mark-recapture models that make the following assumptions [from Krebs (1998)]:

- 1) A closed population. No individuals emigrate or immigrate during the surveys.
- 2) All animals have the same probability of capture in each sampling occasion.
- 3) Marking individuals does not affect their probability of recapture.
- 4) All marks are retained between sampling occasions.
- 5) All marks are detected if individuals are recaptured.

We estimated the total number of sturgeon in the study area and the number of sturgeon present at each unit using the ‘closed captures-full likelihood  $p$  and  $c$ ’ (Otis et al. 1978) model in Program MARK (White and Burnham 1999). This model estimates the probability of capture ( $p$ ), the probability of recapture ( $c$ ), and the number of individuals never caught ( $f_0$ ). We evaluated four models representing constant  $p$  and  $c$ , constant  $p$  and time varying  $c$ , constant  $p =$  constant  $c$ , and time varying  $p =$  time varying  $c$ .

For the estimate of total abundance in the study area, capture data were pooled across sites into three sampling occasions (i.e., sampling occasion one represented the first three net sets at all of the habitat units, sampling occasion 2 represented the fourth through sixth net sets at all the habitat units and sampling occasion 3 represents the seventh through ninth net sets at all the habitat units). For the habitat unit specific abundance estimates we aggregated the detection histories using the same method as above, but for that habitat unit only. Model selection was performed by choosing the model with the highest  $AIC_c$  (Akaike Information Criteria for small samples) weights reported in Program MARK. The four models were evaluated to determine if

violations of the assumptions were driving model results. For example, if marking animals reduced their probability of recapture ( $c$ ) then we would expect the models with the probability of capture ( $p$ ) not equal to the probability of recapture ( $c$ ) to receive the greatest  $AIC_c$ . To make comparisons to the habitat-unit-specific DIDSON abundance estimates we estimated habitat-unit-specific mark-recapture abundances in Program MARK using the model with lowest  $AIC_c$ .

### ***<B>Comparison of Field Effort***

To compare the effort required to perform these two abundance estimation methods, we calculated the number of technician hours expended to gather the respective field data. These two estimations do not include travel time among habitat units or time spent post-processing and analyzing the data. For the mark-recapture estimate, we assumed that three technicians were required; one to pilot the survey vessel and two to deploy and retrieve the nets. All three technicians would participate in sturgeon processing and release. We tallied the total time from our datasheets when nets were deployed and factored an additional ten minutes per captured sturgeon to remove them from the net, process and release. To calculate the total amount of technician hours required to complete the DIDSON field surveys, we assumed that two technicians were required; one to pilot the survey vessel and one to operate the DIDSON. These two technicians were estimated to spend a quarter hour surveying locations where sturgeon were absent and a half hour where sturgeons were present. We were unable to calculate the amount of time required for this task directly from the datasheets or DIDSON files as time was not marked during the data collection and the DIDSON files from locations where sturgeon were absent were not archived.



## <A>Results

Transect simulations indicated that the DIDSON-based sampling method and implemented estimators were unbiased at low, medium, and high densities (Figure 2). Note that the solid lines at the center of the boxes, indicating the mean estimates using the DIDSON, coincided with the light grey lines indicating the true number of sturgeon in the simulation. This was true for estimates of 5, 25, and 50 uniformly distributed Green Sturgeon. Furthermore, these simulations suggest that a determination of the number of sturgeon at a given location can be estimated from a feasible number of transects (Figure 3). For example, when  $N=25$  or  $50$ , we would require approximately seven transects to reach an estimate with an average CV less than or equal to 0.25. However, the estimation method was less precise at low densities ( $N=5$ ).

We detected sturgeon at nine of 65 locations surveyed using the DIDSON. To minimize poaching, we report the habitat units by their unit number and omit any spatial information such as latitude and longitude or river kilometer due to the limited number of locations where Green Sturgeon were present and the fact that these locations are occupied by sturgeon year after year (E. Mora, unpublished data). However, habitat units are numbered moving upstream with unit one being the closest to the river mouth and unit 65 being nearest to the upstream extent of sampling below Blossom Bar.

The abundance of Green Sturgeon was estimated using the DIDSON at all locations where sturgeon were detected. The number of transects performed at each habitat unit varied between three and seven. Using this method, we estimate the total abundance of Green Sturgeon was 223 individuals within the 95% confidence limits of 180 and 266 (Table 1). During this period, sturgeon appeared to congregate in shoals ranging from very few (Unit 44,  $N=6$ ) to many (Unit

15, N=70) individuals. We calculated that DIDSON transects required a total of 37 technician hours to perform.

At seven of the locations where Green Sturgeon were detected, we estimated their abundance using mark-recapture estimation. We performed a total of 81 net sets, for a total soak time of 63 hours and 14 minutes. As a result of the limited three week sample period we were unable to sample habitat unit 35 and 53 using gill-nets. We sampled habitat unit 24 with gill-nets but were unable to capture sturgeon. No recaptures occurred at habitat unit one or 44. Our net sets resulted in 85 sturgeon encounters consisting of 77 individuals (76 Green Sturgeon and one White Sturgeon) and nine recaptures. All recaptures occurred in the same unit as their first capture. The single White Sturgeon was not recaptured and was not included in the mark-recapture estimates. This component of the study required a total of 232 hours of technician hours to complete. Of the four mark-recapture models we implemented to estimate the total number of Green Sturgeon in our study area, the model representing time varying  $p$  = time varying  $c$  resulted in the highest  $AIC_c$  weight of .979 (Table 2). We estimate the number of Green Sturgeon in our study area was 236 within the 95% confidence limits of 150 and 424 (Table 3).

The DIDSON based estimates of abundance agreed with the mark-recapture estimates and generally resulted in tighter confidence intervals. The habitat unit specific DIDSON abundance estimates and their 95 % confidence intervals are almost all within the 95% confidence intervals of the habitat unit specific mark-recapture estimates. The three exceptions are the upper limit of the DIDSON estimate at unit 15, the lower limit of the DIDSON estimate at unit 39 and the lower limit of the DIDSON estimate at unit 60. The DIDSON-based estimate of the total and the

95% confidence interval of this estimate is also within the 95% confidence interval of the mark-recapture estimate. Additionally, the confidence interval of the mark-recapture estimate was generally wider than that of the DIDSON method for the habitat unit specific and total estimates.

## **<A>Discussion**

The DIDSON-based method of abundance estimation improves upon traditional methods that require the capture and handling of individuals in at least two ways. First, this method avoids the negative side effects associated with handling individuals by remotely sensing their presence. This has greatly influenced the ability of researchers to monitor SDPS spawner abundance without the hazard of disturbing spawning aggregations or inducing unnecessary stress related to capture and handling. In mixed species cases where capture and handling of individuals should be avoided, such as in the SDPS, species proportions can be estimated using underwater video camera transects (Groves and Garcia 1998). Green and White sturgeon are easily distinguished using underwater video camera due to their morphological differences such as the presence and number of scutes, color, and patterns of coloration (Moyle 2002). By not handling individuals, researchers may greatly reduce the timeline for field sampling to occur as this ‘hands off’ method is typically exempt from permitting requirements. Second, this method produces an accurate and cost-effective method to evaluate the abundance and distribution of Green Sturgeon. Our comparison showed that with greatly reduced effort, the DIDSON transect based estimator produced superior confidence intervals when compared to the mark-recapture framework. While we did not calculate the empirical probability of the DIDSON’s ability to detect sturgeon within a habitat unit, we suspect it is much higher than that of the capture techniques used in mark-recapture estimation. This is due to the mobile nature of DIDSON transects and the ability of the field technicians to rotate the DIDSON and ‘search’ for sturgeon

during the presence absence surveys. (It should be noted that during abundance estimation transects, the DIDSON should be pointed along the path of the boat to ensure the GPS path represents the viewed area of the DIDSON.) Intrinsicly, it would be much more time intensive, costly and physically invasive for the mark-recapture method to achieve abundance estimates of a similar precision as DIDSON-based transects.

A CV of 0.25 was an arbitrarily chosen level of precision to relay confidence in our final abundance estimate. In comparison, a DIDSON-based estimate of jellyfish density using an unspecified transect estimator resulted in a CV of 1.25 and 1.70 (Han and Uye 2009). In contrast, a stationary deployment of DIDSON at a salmonid counting station resulted in a CV of 0.14 (Cronkite et al. 2006). Thus, we feel that our reference CV near or below 0.25 to be a balance of what is achievable in the field and what is a useful result for the management of this species.

At most locations we performed fewer transects than what our simulations would suggest was optimal. This practice was sufficient to get an accurate estimate of sturgeon abundance in the habitat units. The few habitat unit specific estimates where the lower bounds of the confidence intervals resulted in negative values were the result of a low number of transects. This could have been remedied by performing a greater number of transects during these surveys (Figure 2). Initially we intended to use a bounded counts estimator in combination with DIDSON transects to estimate the number of sturgeon present at each location. Upon further investigation we determined that this approach would violate key assumptions of the bounded counts method (Routledge 1982; Seber 1982). Specifically, it was not theoretically possible to count all animals on a single occasion (transect) as the habitat unit was much wider than the field of view of the

DIDSON. Thus, our simulations show the reductions in transect numbers to be a sacrifice in precision.

The DIDSON-based estimates may not be without bias, however. Any violation of the listed assumptions would result in a bias of the final abundance estimate. Two of the assumptions for the DIDSON-based method, assumptions one and five from above, relate to the movement of individuals. Thus, it is important to supplement DIDSON-based studies with individual based movement rates from tagged fish (acoustic tags, radio tags, etc.) to estimate sturgeon movement patterns during the sample periods. We suspect that our results were not biased by the movement of individuals as Green Sturgeon display typically exhibit small home ranges during our study period (Erickson et al. 2002).

In the future it will be possible to correct the DIDSON-based estimate for the bias induced by moving individuals by using information from tagged fish. Within the spawning grounds of the SDPS, researchers currently operate an array of over 300 acoustic tag detecting monitors (Heublein et al. 2008; Sandstrom et al. 2012) and have surgically implanted acoustic tags into many (300+) Green Sturgeon in either the Central Valley or the mixed stock Columbia River estuary. Currently the Yurok Tribal fishery group operates an array of acoustic tag detecting monitors in the Klamath River (B. McCovey, Yurok Tribal Fisheries Department, personal communication), yet no tag detecting monitors have operated in the Rogue River since the studies of Erickson (2002) and Erickson and Webb (2007).

The assumptions that all locations where the sturgeon are present are surveyed, assumption number four, is best fulfilled by establishing defensible criteria to identify and define the sample units (i.e. all locations greater than 5m deep (Erickson et al. 2002, Thomas et al. 2014)). Then, perform a survey of the study area to identify the locations that satisfy the criteria before sampling with DIDSON. Our study area does omit the region of the Rogue River between Blossom Bar and Rainie Falls, a region accessible to Green Sturgeon yet inaccessible to powered jet boats due to Wild and Scenic Rivers protection. Thus, our study is presented as a comparison of two abundance estimation techniques within an accessible study area and not a run-size estimate for Rogue River Green Sturgeon during 2007.

Assumption number two (100% detection in the DIDSON field of view) is best fulfilled by the use of multiple trained viewers and estimating the precision and bias of their counts similar to the methods implemented in the age and growth literature (Evans and Hoenig 1998). The problem posed by estimating the true, yet unknown, number of growth rings in fish tissues is similar to our challenge of estimating the true, yet unknown, number of sturgeon that passed within the field of view of the DIDSON. We did not explore the impacts of viewer bias on our results, however the opportunity exists to measure how susceptible DIDSON based estimation is to viewer count variation (Evans and Hoenig 1998, Holmes et al. 2006).

Assumption three (the calculated densities are unbiased) is best managed through the use of accurate measurements of the area(s) sampled. That process should involve accurate measurements of transect paths using an appropriate GPS, the careful estimation of sampled area per transect as shown above and the use of GIS to calculate total sampled area. Our study

implemented these guidelines. Thus, we suspect our final estimate of the total number of Green Sturgeon in our study area to be least biased by violations of this assumption.

Our mark-recapture abundance estimates appear to be defensibly implemented in light of the assumptions of this method. It is unlikely that assumption number one (a closed population) was violated as Erickson et al. (2002) displayed that Green Sturgeon are not immigrating into or emigrating from the study area during this time. It is possible, but unlikely, that assumption number two was violated for our habitat unit specific estimate. If sturgeon moved between units between our sampling occasions, this would also bias our estimate of the total number of sturgeon at each location. However, all recaptures occurred in the same location as the initial marking. Our strategy of aggregating the detection histories into three sampling occasions served to address this assumption for the estimate of the total number of Green Sturgeon in the study area. Our estimates appear to be robust against assumption three, marking individuals does not affect their probability of recapture, because the two models with the greatest weights both contain the probability of capture ( $p$ ) being equal to the probability of recapture ( $c$ ). Finally, it is the least likely that assumptions four and five were violated as we double tagged the captured sturgeon.

We will avoid speculating as to why the selected model, time varying  $p =$  time varying  $c$ , contained a time varying component. This fact suggests that an unknown factor was either increasing or decreasing the probability of capture and recapture during each of the sampling occasions potentially increasing or decreasing the final estimates of abundance. The presence of

this unknown factor supports our results that the DIDSON based estimation technique may be better suited to estimate Green Sturgeon abundance.

Estimates of the number of annually spawning adults, population size, and demographic structure of each population of Green Sturgeon will be useful for the management of the species.

Previously, no efforts were being implemented to gather this information. Our results establish the ability to estimate the number of annually spawning adults. To expand the utility of this method it would be feasible to combine this method with estimates of spawning periodicity (Erickson and Webb 2007) or estimates of demographic structure of the populations (Beamesderfer and Simpson 2007) to produce estimates of population size. Further, it would be best to empirically measure the demographic structure of spawning adults via length measurements using DIDSON, a method shown to be feasible by Hightower et al. (2013).

The fine scale locations of detected sturgeon resulting from this method can be used in future habitat assessments of Green Sturgeon. Following multiple presence absence surveys, unit level occupancy rates will emerge (Mackenzie et al. 2006) because it is likely that the same spawning and holding sites will be occupied year after year, allowing for inter-annual variation (Bemis and Kynard 1997). Additionally, presence-absence surveys can be expanded to estimate how frequently habitats shallower than 5 m are occupied. Once patterns of habitat use are identified, that information will be useful to evaluate the degree to which each population is susceptible to spatially correlated catastrophic risk (toxic spills, landslides, poaching etc.) improving the development of potential management scenarios.



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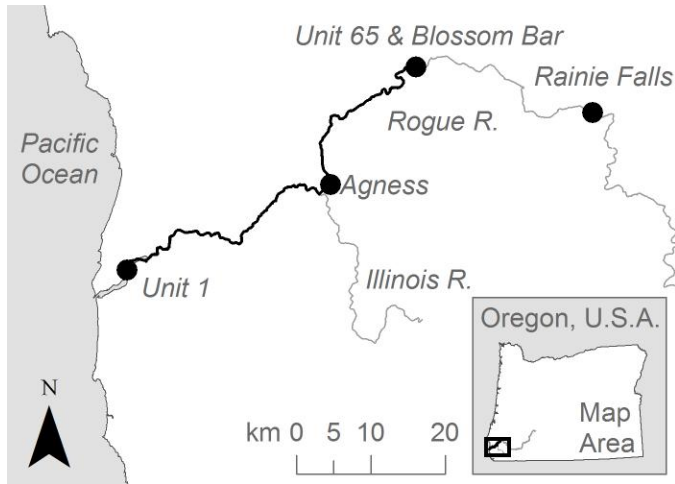


Figure 1: Map of the study area. Study reach shown in black between units 1 and 65. Blossom Bar and unit 65 are in close proximity thus both are shown under the same black marker. The Rogue River upstream of the study area and the Illinois River are shown in grey.



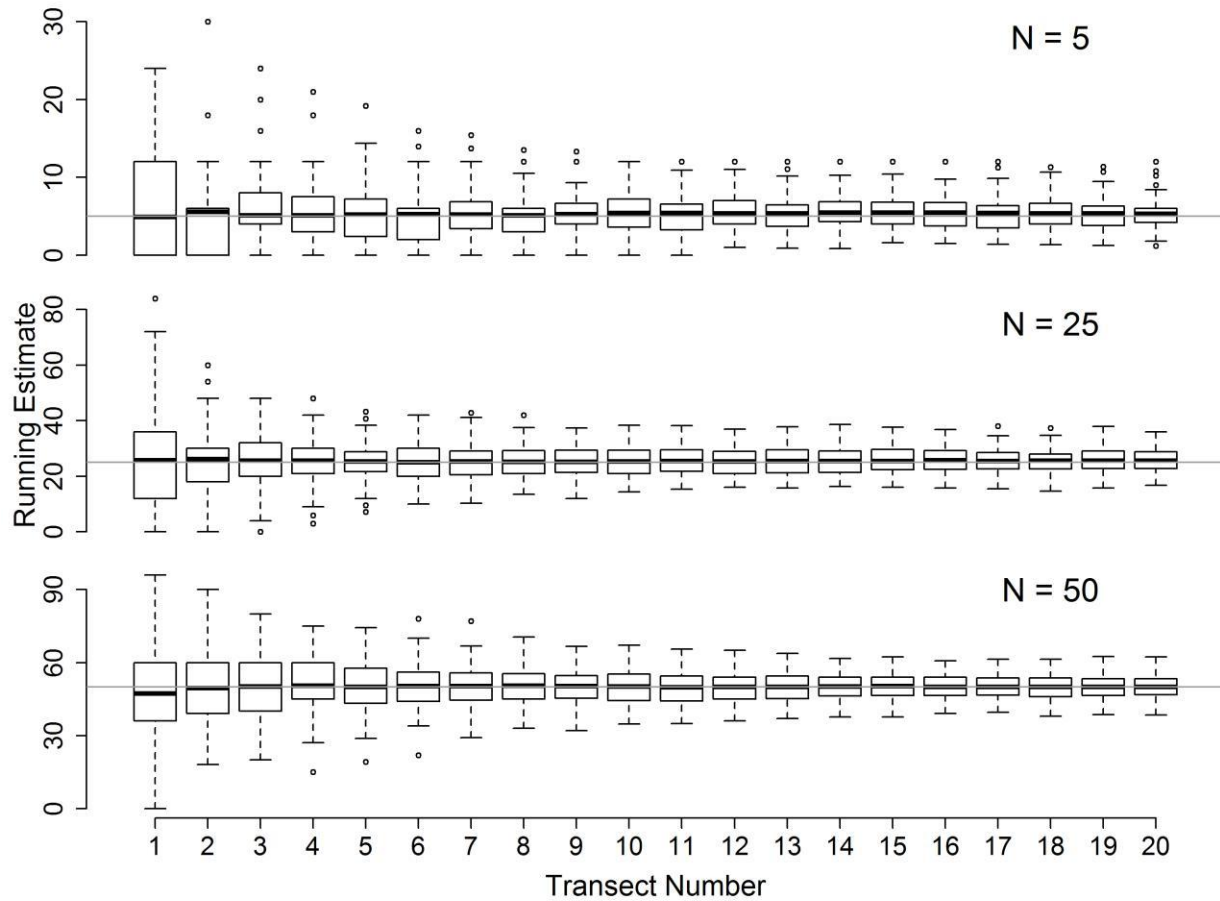


Figure 2: The precision and bias of the DIDSON-based abundance estimate is a function of the number of transects and sturgeon density. One hundred site visits were simulated, each consisting of 20 transects within a 100 m x 300 m stream unit with 5, 25 and 50 uniformly distributed sturgeon. The mean, first and third quartiles of the 100 estimates per transect are plotted with whiskers extending 1.5 the inter quartile range. Outliers are plotted as separate dots outside the whiskers. The true number of organisms in each simulation is shown as the grey line indicating that the mean number estimated equals the true number of organisms.

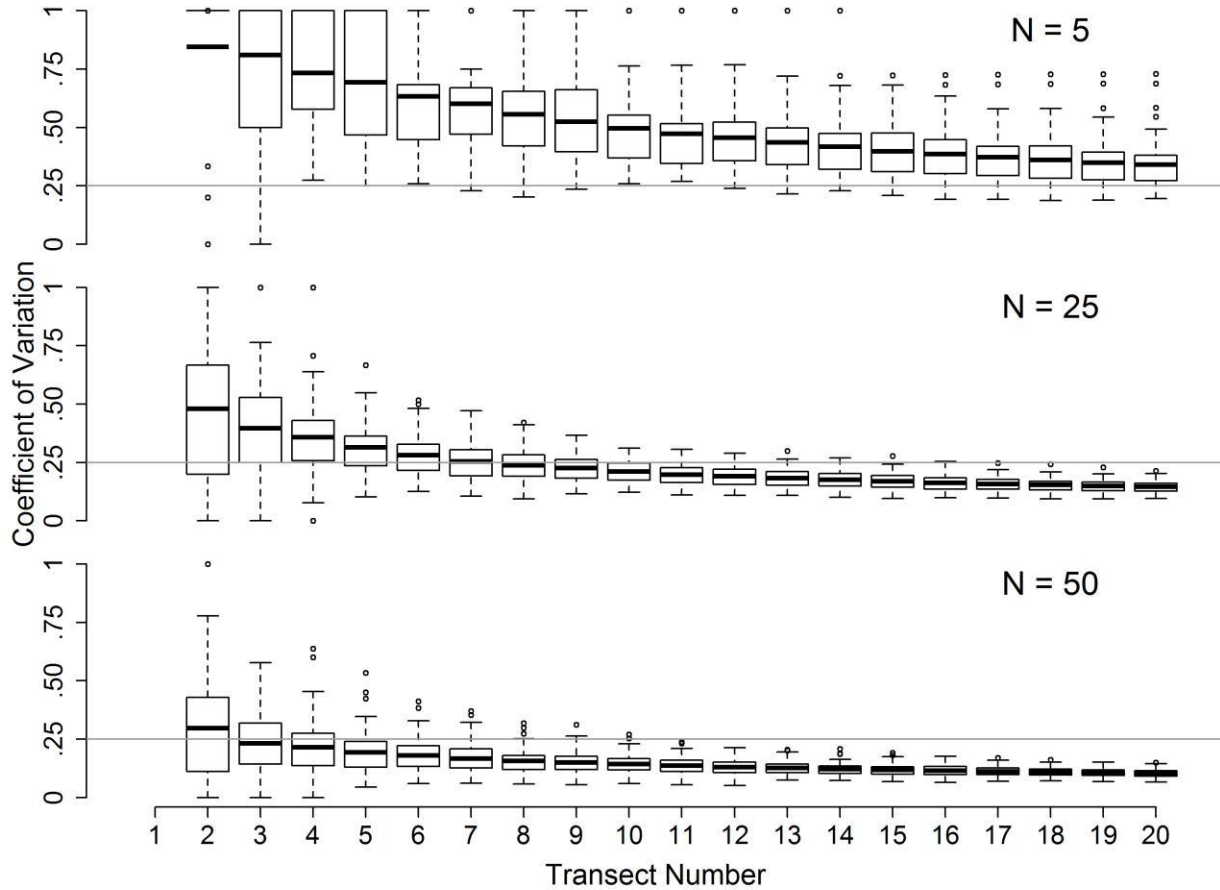


Figure 3: The CV of the DIDSON-based abundance estimate is a function of the number of transects and sturgeon density. One hundred site visits were simulated, each consisting of 20 transects within a 100 m x 300 m stream unit with 5, 25 and 50 uniformly distributed sturgeon. The mean, first and third quartiles are plotted with whiskers extending 1.5 the inter quartile range. Outliers are plotted as separate dots outside the whiskers. The dashed line shows a CV of .25. Here the CV of the estimated total number of sturgeon drops below .25 after a feasible number of transects when N=25 or N=50. The estimation technique is less precise when N=5.

| Unit #         | Number of Transects | N   | SD | Lower 95% CI | Upper 95% CI |
|----------------|---------------------|-----|----|--------------|--------------|
| 1              | 3                   | 20  | 6  | -7           | 47           |
| 15             | 5                   | 70  | 11 | 39           | 100          |
| 24             | 6                   | 7   | 1  | 5            | 9            |
| 35             | 4                   | 7   | 3  | -1           | 15           |
| 39             | 7                   | 21  | 4  | 11           | 30           |
| 44             | 5                   | 6   | 2  | 1            | 11           |
| 53             | 3                   | 34  | 8  | -1           | 69           |
| 57             | 4                   | 24  | 2  | 17           | 29           |
| 60             | 3                   | 38  | 15 | -27          | 104          |
| Total Sturgeon |                     | 226 | 22 | 181          | 270          |
| Green Sturgeon |                     | 223 | 22 | 180          | 266          |

Table 1: Results of DIDSON abundance estimations at each habitat unit where sturgeon were detected. Total Sturgeon is an estimate of the total number of sturgeon detected with DIDSON, regardless of species. Green Sturgeon is an estimate of the total number of Green Sturgeon detected with DIDSON after incorporating an estimate of species proportion. N is an estimate of the total number of sturgeon at each habitat unit.

| Model                           | Delta AIC <sub>c</sub> | AIC <sub>c</sub> Weight |
|---------------------------------|------------------------|-------------------------|
| Time varying p = Time varying c | 0                      | 0.979                   |
| Constant p = Constant c         | 8.51                   | 0.014                   |
| Constant p, Constant c          | 10.44                  | 0.005                   |
| Constant p, Time Varying c      | 12.09                  | 0.002                   |

Table 2: Delta AIC<sub>c</sub> and AIC<sub>c</sub> weights of the four models implemented to estimate Green Sturgeon abundance using Program MARK.

| Unit # | Marked | Recapture | N   | SD | Lower 95% CI | Upper 95% CI |
|--------|--------|-----------|-----|----|--------------|--------------|
| 1      | 3      | 0         | --  | -- | --           | --           |
| 15     | 22     | 4         | 42  | 15 | 27           | 94           |
| 24     | 0      | 0         | --  | -- | --           | --           |
| 35     |        |           |     |    |              |              |
| 39     | 16     | 2         | 35  | 18 | 20           | 108          |
| 44     | 2      | 0         | --  | -- | --           | --           |
| 53     |        |           |     |    |              |              |
| 57     | 11     | 1         | 34  | 29 | 15           | 165          |
| 60     | 22     | 2         | 73  | 44 | 34           | 241          |
| Total  | 76     | 9         | 236 | 66 | 150          | 424          |

Table 3: Mark-recapture estimates of Green Sturgeon abundance at each habitat unit where Green Sturgeon were detected. N is an estimate of the total number of Green Sturgeon. We were unable to sample at units 35 and 53. No recaptures occurred at units one or 44. We were unable to capture sturgeon at unit 24.

### Supplemental Video Caption:

A video export of a typical DIDSON transect. This video displays many challenges inherent in tallying the number of sturgeon detected in a transect. Sturgeon number one is difficult to detect due to a lack of movement and sturgeon re-enter the field of view after being disturbed by the survey vessel. Sturgeon re-entering the field of view were not tallied. Eight sturgeon were detected in this transect. At 0:35, sturgeon number one is visible near the right side of the screen 20-22 m from the lens. At 0:41-0:43, sturgeon numbers two and three are visible near the middle of the screen, 14-18 m from the lens. At 0:47 sturgeon number four is just left of center, 14-16 m from the lens. Sturgeon number five is just right of center, 16-18 m from the lens. Sturgeon number six is on the very left edge of the screen, 16-18 m from the lens. At 0:52, sturgeon number seven is near the right edge of the screen, 16-18 m from the lens. At 0:58, sturgeon number 8 is on the left side of the screen, 13-15 m from the lens.

My research is inherently management driven and the SDPS of Green Sturgeon is a Federally Listed species in need of information to answer management questions. Thus, having successfully piloted the methods of Chapter 1 in the Klamath and Rogue Rivers it was time to apply this useful method to the SDPS, a population whose size was unknown. I was once at a Sturgeon Project Work-team meeting in Sacramento and the NOAA Green Sturgeon Recovery, Coordinator David Woodbury, stated “We don’t know if the population is bigger than a breadbox or smaller than a mouse”. The state of knowledge at the time when I began my thesis sampling was that we had no information about SDPS annual run size, their freshwater distribution, or any estimate of the number of adults in either the SDPS or NDPS. My research established these facts for both populations. The next chapter of this dissertation fully implements the methods described in Chapter 1 to the SDPS and provides a state of reference for future recovery processes.

## Estimating the annual spawning run-size and population size of the Southern Distinct Population Segment of Green Sturgeon, *Acipenser medirostris*

### <A>Abstract

The Southern Distinct Population Segment of Green Sturgeon in the Sacramento River, California is listed as a Threatened Species. We estimated its spawning run and population size in 2010-2015 using Dual Frequency Identification Sonar (DIDSON) sampling, underwater video camera species identification and acoustic tag detections. Spawning run size varied from 336 to 1236 individuals. We estimated total population size to be 17,548 individuals (95% confidence interval = 12,614-22,482). We estimated the number of adults to be 2106 (1,246-2,966), the number of juveniles to be 4,387 (2,595-6,179) and subadults to be 11,055 (6,540-15,571). This study provides the first complete estimate of Sacramento River run size and initiates a time series of abundance useful for Endangered Species Act recovery processes.

### <A>Introduction

Green Sturgeon, *Acipenser medirostris*, are anadromous fish which spawn in three major river systems in California and Oregon (NMFS 2006). The species is separated into two distinct population segments (Israel et al. 2004), which are managed separately by the National Marine Fisheries Service. The Northern Distinct Population Segment (NDPS) consists of individuals that spawn in the Rogue River in southern Oregon and the Klamath River in northern California. The Southern Distinct Population Segment (SDPS) consists of individuals that spawn in the Central



Valley, California. The SDPS was designated as a Threatened Species by the National Marine Fisheries Service in 2006 (NMFS 2006). The NDPS was designated a Species of Concern (NMFS 2006) but the concern for NDPS abundance was buffered by the presence of two spawning stocks. Loss of spawning habitat is considered a detriment to a sustained population of Green Sturgeon in the Central Valley, California (Adams et al. 2007).

The amount of historical habitat available to Green Sturgeon varies by population. The NDPS currently has access to 100% of historically accessible habitat. Spawning in the NDPS consistently occurs in the main stems of the Rogue and Klamath rivers; however, spawning has also been documented in tributaries of the Klamath River, the Trinity and Salmon rivers (Benson et al. 2006). In contrast, the SDPS consists of individuals that spawn almost entirely within a 160 km (100-mile) segment of the Sacramento River below Keswick Dam, which forms a barrier to passage (Adams et al. 2007). In addition, SDPS spawning was documented in the Feather River during June, 2011 (Seesholtz et al. 2015) indicating that Green Sturgeons can spawn in major Sacramento River tributaries. It is probable that the SDPS historically spawned in currently inaccessible portions of rivers above dams in the American, Feather and Yuba rivers. Today, flow regulation and habitat fragmentation likely constrain their current spawning distribution (Mora et al. 2009).

NMFS (2006) identified the lack of information describing the total number of individuals in each of the populations as a potential risk factor for both populations. No direct estimates of population abundance of either DPS existed. For each DPS, the status designation was prompted by a steady decline in other indicators of abundance. These indicators include 1) an indirect

abundance estimates based on the proportion of Green Sturgeon caught together with White Sturgeon, *Acipenser transmontanus*, by the California Department of Fish and Wildlife 2) the annual catch in the Yurok tribal Green Sturgeon fishery, and 3) catch per unit effort estimates from a commercial Columbia River sturgeon fishery. White sturgeon coexist with green sturgeon in the Sacramento River but are much more abundant (Moyle 2002). While there is a body of knowledge about the life history timing and potential demographic structure of the species (Beamesderfer and Simpson 2007), DPS-specific estimates of adult abundances necessary to facilitate future status assessments have yet to be produced. Thus, the objectives of this study were to estimate the number of annually migrating SDPS Green Sturgeon and to estimate the number of individuals in the population in the Sacramento River.

#### <A>Methods:

#### <B>Study Site

The Sacramento River is the largest river in California, draining the northern 71,000 km<sup>2</sup> of the Central Valley. Our study took place within a 155 km reach between the Anderson-Cottonwood Irrigation District Dam (rkm570) and the Highway 32 overcrossing (rkm 415) during the months of June and July of 2010 – 2015 (Figure 1). We calculated river km as the distance upstream from the Golden Gate Bridge.

Our sample sites consisted of the 125 locations greater than 5m deep described in Thomas *et al.* (2014), based on a meso-habitat survey by the U.S. Bureau of Reclamation beginning in January of 2008 and completed May 2010. In the Rogue River, NDPS Green Sturgeon congregate in locations greater than 5m deep (Erickson et al. 2002). Thus, Thomas *et al.* (2014) and our study chose a 5m depth criterion to identify potential congregating locations within the Sacramento River. The Bureau of Reclamation survey identified 125 discrete habitat units fulfilling this criterion, a portion of which were occupied by Green Sturgeon carrying acoustic tags (Thomas et al. 2014). A subset of these surveyed sites were confirmed as spawning locations by Poytress *et al.* (2013).

#### <B>Run Size Estimate

#### <C>Estimating Abundance with DIDSON:

We modified the presence-absence and abundance estimation methods described by Mora *et al.* (2015) to estimate the abundance of annually migrating Green Sturgeon in the Sacramento River. Our modification was that we first censused the sample sites to determine the presence or absence of sturgeon using Dual Frequency Identification Sonar (DIDSON) [Sound Metrics, Bellevue WA]. DIDSON is an acoustic camera that operates like a medical ultrasound, allowing researchers to see video like images of ensonified fish, submerged objects and substrate. The presence-absence surveys were initiated during the first week of June, generally lasted two weeks and systematically occurred moving upstream from the most downstream sample site. We then estimated the abundance of sturgeon at each of the occupied locations over

one to three days. Depending on the year, the DIDSON surveys were either performed by one or two teams working concurrently. However video camera sampling (See Estimating Species Proportion below) was always performed by a single team. Our other modification from the methods of Mora *et al.* (2015) allowed us to account for some of the potential bias inherent in the movement of individual sturgeon during the sample period.

#### <C>Estimating Species Proportion:

Both Green Sturgeon and White Sturgeon spawn in the Sacramento River (Kohlhorst 1976). Telemetry studies suggest that their spawning habitats are separated in time and space (Miller 1972, Shaffter 1997); however, other sources (Israel and Klimley 2008) relay the possibility that White Sturgeon may be present in study units during our surveys. As these two species are indistinguishable in the DIDSON images, we used underwater video camera transects to estimate the relative proportions of Green and White Sturgeons at locations of detected sturgeon presence. To gather visual sturgeon detections suitable for species identification, we towed an underwater video camera (Splash Cam Deep Blue Pro, Ocean Systems, Inc., Everett, WA) attached to a 10kg sounding weight at locations where sturgeon densities were sufficiently high enough to ensure detections (Groves and Garcia 1998). The standard definition (720p) video feed from the camera was recorded onto DVD (2010, 2011) or digital video tape (2012-2015) for later analysis, and viewed real-time aboard the survey boat to avoid collisions with sturgeon. During 2012-2015 we fitted the towed cameras assembly with a high definition (1080p) underwater video camera (GoPro Hero2, GoPro, Inc., San Mateo, CA) to record a greater field of view compared to the

Deep Blue Pro. These species proportion surveys occurred the week after the abundance estimating DIDSON surveys.

We reviewed the video files, tallied the number of sturgeon detections and assigned them as Green Sturgeon, White Sturgeon, or Undetermined Species. Our criteria for identifying sturgeon species are below and in order of decreasing precedence (Moyle 2002):

- 1) 8-11 dorsal scutes: *A. medirostris*; 11-14 dorsal scutes: *A. transmontanus*
- 2) 23-30 lateral scutes: *A. medirostris*; 38-48 lateral scutes: *A. transmontanus*
- 3) Presence of a post-dorsal scute: *A. medirostris*
- 4) Ventral Green Stripe: *A. medirostris*
- 5) Presence of a lateral Green stripe between pectoral-pelvic fins: *A. medirostris*
- 6) If none of the above criteria are discernable: Unknown species.

For each year of the survey, we estimated the proportion of detected sturgeons that were Green Sturgeon as a binomial proportion ( $\hat{P}_G$ ) of the number of sturgeon-camera interactions identified as Green Sturgeon ( $N_G$ ) to the number of sturgeon-camera interactions identified to species ( $N_c$ ).

This was an annually and geographically pooled estimate:

EQ(1) 
$$\hat{P}_G = \frac{N_G}{N_c}$$

with variance:

EQ(2) 
$$\hat{V}(\hat{P}_G) = \frac{\hat{P}_G(1 - \hat{P}_G)}{N_c}$$

<C>Estimating Migration Patterns with Telemetry Data:

Individual Green Sturgeon migrate into and out of the survey area at varying times during each spawning year, so that during any given survey the entire spawning run may not be in the survey area. Mora *et al.* (2015) described assumptions of our abundance estimation technique that, when violated, will impart bias to the final estimate. They recommended using individual based information describing migration patterns to correct for these potential sources of bias. To account for the effects of this bias on our estimates of abundance, we relied on detections of acoustically tagged Green Sturgeon in the study area. These individuals (n=288) were tagged in previous studies (Heublein et al. 2008, Vogel 2008, Lindley et al. 2011, Thomas et al. 2014) and detected by an array of tag detecting monitors maintained by the Biotelemetry laboratory of the University of California, Davis (UCD). We utilized these apparent migration patterns to estimate the quantity of two pools of individuals that we were unable to detect during our DIDSON surveys: 1) the proportion of annual migrants that exited the study area previous to our abundance estimate, and 2) the daily average proportion of individuals migrating between units during June and July.

<C>Proportion of Annual Migrants That Had Exited the Study Area:

We summarized individual Green Sturgeon detections by week and coded them as either present or having already exited the study site to estimate the proportion of annual migrants that had exited the study area prior to our abundance estimate. This was determined for individuals not tagged in the same spawning year as being summarized with the exception of 2011 wherein only two previously tagged fish entered the study area. For the year 2011, we included the exit dates of 22 individuals tagged during that spawning year (Thomas et al. 2014). For all years, the estimate of proportion of individuals that had exited the study system before our abundance estimate occurred was calculated as a binomial proportion ( $\hat{P}_P$ ) of the number of individuals that had exited the study system by the week of our abundance surveys ( $N_S$ ) to the number of total annual migrants detected on the hydrophone array that year within the study area ( $N_M$ ):

$$\text{EQ(3)} \quad \hat{P}_P = \frac{N_S}{N_M}$$

with variance:

$$\text{EQ(4)} \quad \hat{V}(\hat{P}_P) = \frac{\hat{P}_P(1 - \hat{P}_P)}{N_M}$$

We then utilized the total number of detected sturgeon from the DIDSON transects ( $\hat{T}$ , from Mora *et al.* 2015, equation 5.) to estimate the total number of individuals that had exited our study system before our abundance surveys ( $\hat{N}_E$ ) as:

$$\text{EQ(5)} \quad \hat{N}_E = \left( -\frac{\hat{T}}{\hat{P}_P - 1} \right) \hat{P}_P$$

The variance of  $\hat{N}_E$  was calculated using the Delta Method as in Mora et al. (2015):

$$\text{EQ(6)} \quad V(\hat{N}_E) = [(\hat{P}_P)^2 \cdot \hat{V}(\hat{T})] + [(\hat{T})^2 \cdot \hat{V}(\hat{P}_P)] + [\hat{V}(\hat{P}_P) \cdot \hat{V}(\hat{T})]$$

Equations five and six result in an annual estimate of the total number of annual migrants that had exited the study area prior to our sampling, and the estimated variances of these totals.

#### <C>Number of Individuals Migrating Between Habitat Units:

To estimate the daily average number of individuals migrating between habitat units in the study area during June and July of each year, we queried the UCD Laboratory's database for Green Sturgeon detections occurring during these months, between the hours of 7am and 7pm (the daily time period of sampling) and only at hydrophones not located directly in the sample sites. We estimated a daily quantity ( $\hat{P}_I$ ) as a binomial proportion of the number of unique individuals detected, and assumed to be migrating between units ( $N_D$ ), to those present in the study area and not detected during that day and thus assumed to be within the habitat units ( $N_M$ ).

$$\text{EQ(7)} \quad \hat{P}_I = \frac{N_D}{N_M}$$

with variance:

$$\text{EQ(8)} \quad \hat{V}(\hat{P}_I) = \frac{\hat{P}_I(1 - \hat{P}_I)}{N_M}$$



To estimate the annual average proportion of individuals that were moving between units during our sample period, we calculated the average ( $\bar{P}_I$ ), of the daily estimates  $\hat{P}_I$  as:

$$EQ(9) \quad \bar{P}_I = \sum_i^n \frac{\hat{P}_I}{n}$$

With variance:

$$EQ(10) \quad V(\bar{P}_I) = \sum_i^n \frac{\hat{V}(\hat{P}_I)}{n^2}$$

Then for each year, we calculated the total number of individuals that were transiting between sample sites during our abundance surveys ( $\hat{N}_T$ ) as:

$$EQ(11) \quad \hat{N}_T = \left( -\frac{\hat{T}}{\bar{P}_I - 1} \right) \bar{P}_I$$

The variance of  $\hat{N}_T$  was calculated using the Delta Method as in Mora et al. (2015):

$$EQ(12) \quad V(\hat{N}_T) = [(\hat{P}_I)^2 \cdot \hat{V}(\hat{T})] + [(\hat{T})^2 \cdot \hat{V}(\hat{P}_I)] + [\hat{V}(\hat{P}_I) \cdot \hat{V}(\hat{T})]$$

Equations 11 and 12 result in annual estimates of the total number of individuals migrating between units during our annual sample periods and the estimated variances of these totals.

The means and variances of these three estimated annual quantities ( $\hat{T}, \hat{N}_E, \hat{N}_T$ ) were then summed to represent the total number of Green Sturgeon that migrated during each year and the estimated variances of those totals.

### <B>Population Estimate

To estimate the number of mature adults in the SDPS we first had to estimate two quantities: the mean and variance of run sizes over a six year period and the distribution of interannual spawning frequencies.

Green sturgeon are iteroparous and individuals do not make spawning migrations every year. To estimate the distribution of temporal intervals between spawning migrations from repeat spawners we again turned to the detection record of acoustically tagged Green Sturgeon. The detection database was queried for all Green Sturgeon performing a spawning migration. Individuals were considered to have completed a spawning migration in a given year if they were detected by a tag detecting monitor in our study area that year. We then calculated the interval, in years, between spawning migrations for 41 individuals that had spawned more than once. The identified distribution was used as an estimate of SDPS spawning periodicity. The mean,  $\bar{S}_{GS}$  and variance of this distribution is  $V(\bar{S}_{GS})$  were calculated using the standard estimators for a sample mean and variance.

$$EQ(13) \quad \bar{S}_{GS} = \frac{1}{n} \sum_i^n x_i$$

$$EQ(14) \quad V(\bar{S}_{GS}) = \frac{1}{n-1} \sum_i^n (x_i - \bar{x})^2$$

We then estimated the average run size of SDPS Green Sturgeon by calculating the six year geometric mean of our run size estimates using the following equations. The average run size ( $\bar{T}_G$ ) was calculated as:

$$EQ(15) \quad \bar{T}_G = \sqrt[6]{\prod_i^6 \hat{T}}$$

with variance:

$$EQ(16) \quad V(\bar{T}_G) = \sum_i^6 \frac{\hat{V}(\hat{T})}{6^2}$$

We estimated the total number of adults in the SDPS ( $\hat{N}_A$ ) by multiplying the average run size ( $\bar{T}_G$ ) by the estimated average spawning periodicity ( $\bar{S}_{GS}$ ).

$$EQ(17) \quad \hat{N}_A = \hat{S}_{GS} \bar{T}_G$$

The variance of  $\hat{N}_A$  was calculated using the Delta Method as in Mora *et al.* (2015):

$$\text{EQ(18)} \quad V[\hat{N}_A] = (\hat{S}_{GS})^2 \hat{V}[\bar{T}_G] + (\bar{T}_G)^2 \hat{V}[\hat{S}_{GS}] + \hat{V}(\bar{T}_G) \hat{V}(\hat{S}_{GS})$$

Beamesderfer and Simpson (2007) determined that the SDPS Green Sturgeon population, given the assumptions of a population at equilibrium, would have an expected life stage distribution of 25% juveniles, 63% sub-adults and 12% adults. The juvenile life history stage was defined by Beamesderfer and Simpson (2007) as “fish during freshwater rearing prior to migration to the ocean (generally one to three years of age and 0-60 cm in length).” Adults were defined by the authors as “fish larger than the median size and age of female maturation (approximately 165 cm and 20 years of age).” The sub-adult life history stage refers to individuals between these two age classes. Combining the proportions provided by Beamesderfer and Simpson (2007) with our estimate of the number of adults in the SDPS, we estimated the number of individuals in the juvenile and sub-adult life history classes.

## <A>Results

Abundance sampling occurred over one to three days from mid-June to early July each year (Table 1). The number of days required to sample the occupied habitat units varied between years due to the number of cumulatively occupied units and the varying number of sampling teams. During 2010, 2011 and 2012 two crews worked together to sample different units concurrently; however, in 2013 through 2015 sampling was performed by one crew.

Table 2 displays the estimates of the total number of sturgeon present considering only the DIDSON transect estimate of abundance. As estimates of run size for each year, these values are uncorrected for the bias imparted due to violations of the assumptions listed in Mora *et al.* (2015).

Annual estimates of the proportion of Green Sturgeon in our study area calculated from video camera transects ranged from 0.98 to 1 (Table 3). Of the 699 sturgeon interactions captured on video, 390 were identifiable to species and of those, only two were White Sturgeon. These two White Sturgeon observations occurred during one year and were captured on the same day in the same location on the same video camera transect. Otherwise, it is apparent that the majority of sturgeon detected in our study area were Green Sturgeon.

An estimate of the proportion of annual migrants that had left the study area before our abundance surveys were performed ranged from 0.00 to 0.57 (Table 4). Recall that the 2010-2013 sampling occurred during the period of 3-10 June of each year while 2014 occurred a few weeks later, during the period of 30 June – 2 July. The 2015 sampling occurred during the period June 24 – June 26.

An estimate of the proportion of Green Sturgeon in transit between sample sites during DIDSON surveys ranged from 0.004 to 0.017 (Table 5).

The estimates of annual run size accounting for the proportion of sturgeon transiting between sites or out of the study area are shown in Table 6. These values represent the total number of

adult Green Sturgeon that entered our study area each year. These values do not include the number of migrants that entered tributaries of the Sacramento River such as those documented by Seesholtz *et al.* (2015). The average run size was calculated to be 571 with the 95% confidence limits of 529 and 613.

The detections of 42 repeat migrations of 41 individuals displayed a spawning interval of 2 to 6 years. The mean spawning periodicity was 3.69 years with a variance of 0.56 (Figure 2).

We directly estimated the number of adults in the SDPS to be 2,106 within the 95% confidence limits of 1,246 and 2,966. Applying the life history proportions of Beamesderfer and Simpson (2007), we estimated there to be 4,387 juveniles within the 95% confidence limits of 2,595 and 6,179 and 11,055 sub-adult within the 95% confidence limits of 6,540 and 15,571, for a total population estimate of 17,548 SDPS Green Sturgeon within the 95% confidence limits of 12,614 and 22,482 individuals.

## <A>Discussion

We estimate that during the study period there were between 1,246 and 2,966 SDPS Green Sturgeon in the reproductive portion of the population. We regard this as a fairly realistic estimate of SDPS Green Sturgeon population size because it overcomes two issues that hampered earlier estimates: a limited sample region (Israel and May 2010), and estimating the abundance of Green Sturgeon based on the ratio of Green to White sturgeon numbers in a White Sturgeon sampling study (U.S Fish and Wildlife Service 1995, Adams et al. 2007). Our study, if

anything, likely underestimates the SDPS abundance because it did not include the recently documented spawners in the Feather River, as determined from a collection of thirteen eggs from Green Sturgeon (Seesholtz et al. 2015). Future population estimates of adult SDPS Green Sturgeon should coordinate DIDSON sampling in the mainstem Sacramento with concurrent sampling in other Central Valley tributaries.

Our estimates of juvenile, subadult, and total SDPS green sturgeon numbers are less reliable because they are based on the ratios in Beamesderfer and Simpson's (2007) modeling study which combines data from the NDPS and SDPS. Their estimate of percentage of juvenile sturgeon is particularly uncertain because so little is known about this life stage. However, this study provides a tractable first-order estimate of total abundance suitable for future recovery planning, information that was previously unknown.

The sample period between 2010 and 2011 occurred during a major change in the habitat availability for spawning Green Sturgeon in the Sacramento River. During the initial two years of this study Red Bluff Diversion Dam, located roughly half way along the survey reach, operated as a complete barrier to upstream migration for a portion of the spawning season, by keeping its gates on the main river closed. During 2010 the dam prevented passage of fish between May 15<sup>th</sup> and September 15<sup>th</sup>. During 2011, the dam prevented passage between June 15<sup>th</sup> and September 15<sup>th</sup>. After 2011, the gates were permanently opened for the remainder of the study. Because Red Bluff diversion dam is located approximately in the middle of the sample area, this management change made accessible many habitat units upstream of the dam. While this study does provide the beginning of a useful time series of Green Sturgeon habitat

occupancy, the years 2010 and 2011 should be treated separately in any analysis of distribution (Flowers and Hightower 2013).

The Demographic Recovery Criteria, under development by NMFS as part of the SDPS Green Sturgeon Recovery Plan, contain quantitative targets of population size that would, if met, warrant delisting under the Endangered Species Act. The criterion requires an estimated adult population of 3,000 individuals that 'equates to an average yearly run of 833 fish' (Joe Heubline NMFS Green Sturgeon Recovery Coordinator, Personal Communication). Our results show that the population is not yet reached the desired 3000 spawning adults in the population. Note, the value of 833 was determined by dividing the target number of adults in the population, 3000, by the average spawning periodicity, 3.60 years, calculated by the NMFS recovery coordinator. Implementing the average annual spawning periodicity calculated by our analysis, 3.69 years, the desired average run size would be 813 adults per year. The target annual run size is sure to change in the future as more repeat migrations contribute to the estimate of annual spawning periodicity.

The criteria states that 'each annual spawning run must be comprised of a combined total, from all spawning locations, of at least 500 adult fish.' That recovery target was met during four of six years of our survey; however the criteria provides no guidance on the interpretation of confidence intervals. For example the 2011 estimate of 334 adult spawners has a 95% confidence interval spanning 273-395 adults, clearly not reaching the 500 adult fish criteria. A less clear result occurred in 2012 when 597 adult spawners were estimated to have migrated into the study area. The 95% confidence intervals of that estimate span 499-695 adults, almost



entirely within the desired criteria. The Demographic Recovery Criteria could be clarified to specify if just the point estimate of adult run size and population size, the entire confidence interval, or just a majority of the confidence interval is used to satisfy the recovery criteria.

It is clear that further implementation of DIDSON based surveys that measure the abundance and distribution of Green Sturgeon during their spawning period will provide information crucial to the evaluation so SDPS Green Sturgeon status. Two of the five Demographic Recovery criteria describe criterion based on either abundance (annual run size, total population size) or distribution (successful spawning in at least two rivers within their historical range). Spawning has been historically detected in the Feather River (Seesholtz et al. 2015) and future coordinated DIDSON surveys of the Feather and Sacramento Rivers is planned.

This study provides additional evidence that sturgeon in the study area during June and July are almost entirely Green Sturgeon. The only exception to this expectation was the two White Sturgeon detected in 2013. Given the findings of Miller (1972) and Shaffter (1997), this pattern was not surprising; however, we had expected a larger proportion of the detected sturgeon to be White Sturgeon based on Israel and Klimley (2008) and self-reporting by recreational fishermen to the California Department of Fish and Wildlife. Other evidence provides support for Green Sturgeon dominance. For example, all sturgeon larvae and juveniles that were captured in a screw trap operated at Red Bluff Diversion Dam were identified as Green Sturgeon (Poytress et al. 2014). In addition, initial results of Green and White Sturgeon migration studies by the UCD Biotelemetry Laboratory support our findings (Emily Miller, U.C.Davis, personal communication).

The high run size estimate from 2014 stands out as an obvious outlier. The sampling for the 2014 estimate occurred roughly two weeks later in the spawning season than the other annual estimates. Otherwise, all aspects of the study design were the same during 2014 as they were during previous years. For the 2014, two components of the estimate of run size were the greatest for any year of our study: the total number of sturgeon detected via DIDSON transects and the proportion of individuals that had left the study system before our DIDSON sampling began. These two factors clearly combined to inflate the estimate of run size but we consider their estimated values as valid because measurements from all years were performed uniformly. It is worth noting that the 2014 spawning season occurred during a major drought in California although it is unknown how environmental factors, such as reduced flow, influence run size and Green Sturgeon spawning migrations. As our study continues and our time series expands, we plan to investigate these questions.

Finally, because our model is reliant on individual based migration information, it is crucial that tagging of individuals with long lasting acoustic tags continue to be conducted to inform population monitoring efforts into the future. Population monitoring of the SDPS of Green Sturgeon is a crucial aspect to understand the status of the species. DIDSON sampling and acoustic tagging appear to be the most efficient and least invasive methods to track the SDPS Green Sturgeon status. It would be important to know, for example, if the greater numbers of adults observed in 2014 represents a reproductive cohort or a response to environmental changes.

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| Year | Sample Date         |
|------|---------------------|
| 2010 | 6/17                |
| 2011 | 6/16                |
| 2012 | 6/14, 6/15          |
| 2013 | 6/10, 6/11,<br>6/12 |
| 2014 | 6/30, 7/1, 7/2      |
| 2015 | 6/24,6/25,6/26      |

Table 1: Dates when abundance estimating samples occurred.



| Year | N   | ± 95% CI |
|------|-----|----------|
| 2010 | 245 | 63       |
| 2011 | 220 | 41       |
| 2012 | 329 | 56       |
| 2013 | 338 | 61       |
| 2014 | 526 | 64       |
| 2015 | 423 | 59       |

Table 2: The estimated total number of sturgeon resulting from the DIDSON transects, uncorrected for bias due to violations of assumptions.

| Year | N Green | N White | Unknown | P (Green) | Variance |
|------|---------|---------|---------|-----------|----------|
| 2010 | 76      | 0       | 47      | 1.00      | 0.0000   |
| 2011 | 39      | 0       | 40      | 1.00      | 0.0000   |
| 2012 | 50      | 0       | 57      | 1.00      | 0.0000   |
| 2013 | 88      | 2       | 87      | 0.98      | 0.0002   |
| 2014 | 100     | 0       | 64      | 1.00      | 0.0000   |
| 2015 | 37      | 0       | 26      | 1.00      | 0.0000   |

Table 3: The number of each species detected on video camera and the mean and variance of the estimated species proportions.

| Year | N Migrants | N Exit | Proportion Not In River | Variance |
|------|------------|--------|-------------------------|----------|
| 2010 | 9          | 5      | 0.56                    | 0.027    |
| 2011 | 24         | 8      | 0.33                    | 0.009    |
| 2012 | 18         | 8      | 0.44                    | 0.014    |
| 2013 | 14         | 0      | 0.00                    | 0.000    |
| 2014 | 14         | 8      | 0.57                    | 0.017    |
| 2015 | 32         | 14     | 0.44                    | 0.008    |

Table 4: The number of sturgeons implanted with acoustic tags that were detected as leaving our study area each year before the initiation of our abundance surveys.

| Year | Proportion In Transit | Variance |
|------|-----------------------|----------|
| 2010 | 0.004                 | 4.07E-06 |
| 2011 | 0.02                  | 1.37E-05 |
| 2012 | 0.015                 | 7.72E-06 |
| 2013 | 0.013                 | 1.41E-05 |
| 2014 | 0.017                 | 1.66E-05 |
| 2015 | 0.01                  | 4.14E-06 |

Table 5: The estimated average daily proportion of tagged sturgeon migrating between sample sites during the month of June and July.

| Year | N    | ± 95%<br>CI |
|------|------|-------------|
| 2010 | 552  | 109         |
| 2011 | 334  | 61          |
| 2012 | 597  | 98          |
| 2013 | 335  | 61          |
| 2014 | 1236 | 157         |
| 2015 | 756  | 98          |

Table 6: The estimated number of Green Sturgeon that migrated into the study area between 2010 and 2015.

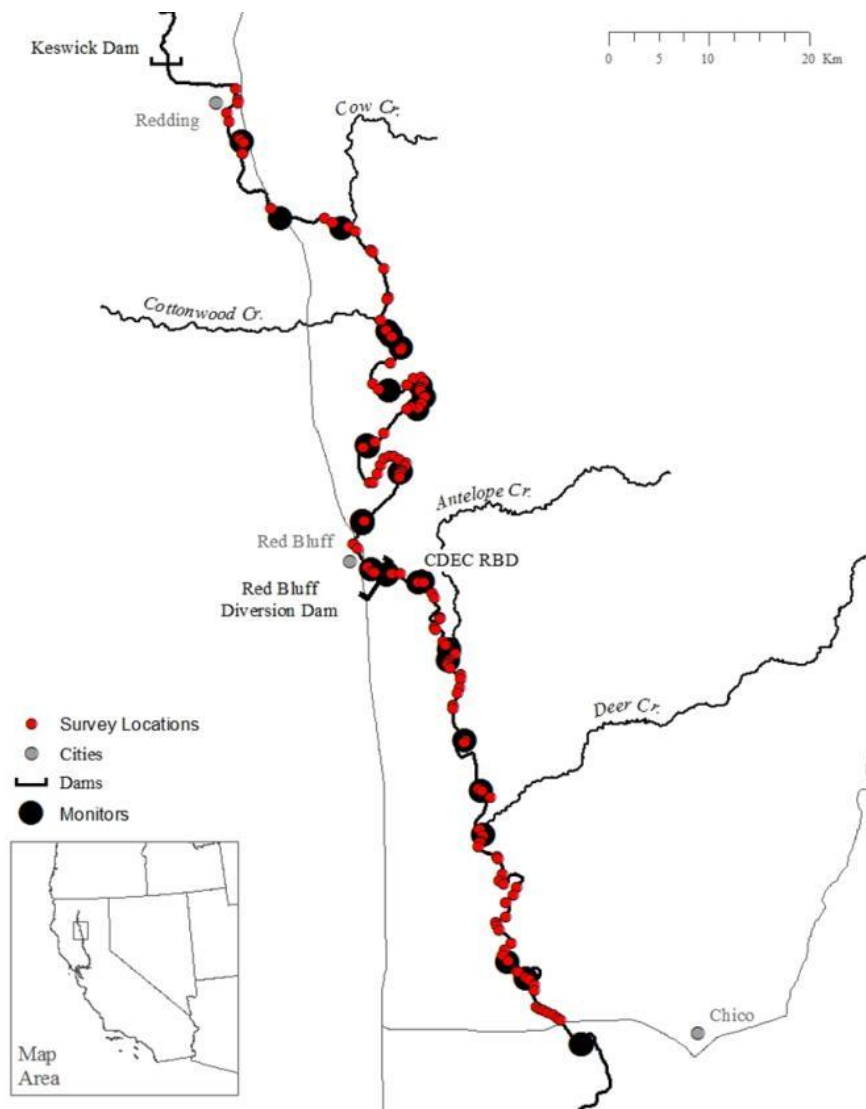


Figure 4: The Sacramento River showing the sample sites as red dots and tag detecting monitors as black dots.

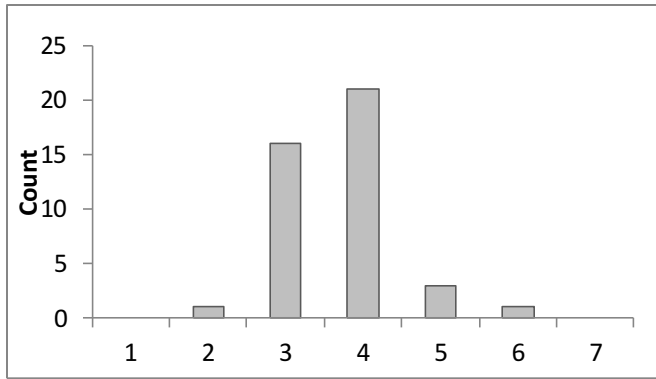


Figure 2: Histogram of spawning periodicity of acoustically tagged Green Sturgeon.

Again, my research is very management driven. At the same Sturgeon Project Work-team meeting a concern was raised that the management of the Sacramento Rivers water temperature regime, structured for the benefit of spawning Winter Run Chinook (*Oncorhynchus tshawytscha*), was having a deleterious effect on the growth of juvenile Green Sturgeon. An analysis presented at one meeting proposed that the thermal conditions in the Sacramento River were cooler within the spawning range of adult Green Sturgeon as compared to the much warmer regions of the Klamath and Rogue Rivers. The presentation attempted to show that this trend was visible in the apparent growth rate of juveniles in screw trap length measurements of sampled individuals. This concern stimulated the idea that it may be possible to model this phenomenon and thus I embarked on this idea.

We were fortunate that two crucial pieces of information were recently produced. First, Dr. Nann Fangué had recently completed experiments analyzing the growth of juvenile Green Sturgeon as influenced by different food and ration treatments. Second, the National Marine Fisheries Service in Santa Cruz, Ca had completed a water temperature model of the Sacramento River that described water temperature at fine spatial and temporal scales. Thus, the model described here offers many potential extensions to answer future management questions related to the temperature management of the Sacramento River and the resulting effects on juvenile Green Sturgeon growth and survival.



Evaluating the effect of temperature and flow management on the growth and survival of early life history Green Sturgeon (*Acipenser medirostris*)

### **<A>Abstract**

We developed an individual based model that tracks growth and survival of juvenile Green Sturgeon during the first 45 days of their outmigration. Water temperature had the greatest influence on total biomass produced while migration rate had a lesser effect on produced biomass. We then utilized this model to evaluate the expected productivity of spawning events varying in time and space. We determined that after the removal of Red Bluff Diversion Dam, Green Sturgeon now have access to the most productive regions of their spawning habitat below Keswick Dam.

### **<A>Introduction**

In 1945, the construction of Shasta Dam on the Sacramento River marked a pivotal time in the development of the complex conveyance system that now delivers water to two thirds of California's citizens and supports an important agricultural industry. Reservoirs are an essential component of this water management system, because currently more than 1500 dams exist in the State of California (Goslin 2005). Dam construction can impact many physical and biological phenomena of freshwater ecosystems (Ward and Stanford 1983), including water temperature and ecological community structure. These impacts were noted as early as four years after the construction of Shasta Dam. Moffett (1947) identified the consequences of creating the

dam: such as cooler summer temperatures and warmer winter temperatures in the river downstream of the dam, reflecting increased flow releases for irrigation in summer and reduced flows in winter for water storage.

An altered temperature regime in the Sacramento River remains today, although it is partly the result of structured water releases to support the conservation of fish species listed under the Endangered Species Act (ESA): winter-run Chinook salmon (*Oncorhynchus tshawytscha*), spring-run Chinook salmon (*Oncorhynchus tshawytscha*), California Central Valley steelhead (*Oncorhynchus mykiss*), and Green Sturgeon (*Acipenser medirostris*) [National Marine Fisheries Service 2009, Sacramento River Temperature Task Group 2014]. However, the current temperature regime may differentially benefit listed species, which may have conflicting water temperature requirements. In this study, we describe the differential growth and survival of Green Sturgeon under various riverine conditions and explore how structured water releases influence vital rates of juveniles.

The Green Sturgeon is an anadromous species that spawns in the Sacramento and Feather Rivers (Southern Distinct Population Segment- SDPS) and in the Rogue and Klamath Rivers (Northern Distinct Population Segment – NDPS) (Adams et al. 2007, Seesholtz et al. 2015). The SDPS is listed as a Threatened Species by the U.S. Endangered Species Act and the NDPS is listed as a species of concern (NMFS 2006, Adams et al. 2007). The two populations differ in population size and in the physical environments of their spawning rivers (Adams et al. 2007). Spawning for Green Sturgeon takes place March through July (Moyle 2002).

Dam construction has altered water temperatures in all three spawning rivers of Green Sturgeon. The Klamath River experiences increased summer water temperatures due to reduced inflows from the Trinity River at Lewiston Dam and along the mainstem Klamath River downstream of Iron Gate Dam. During May and June from 1965 to 2014, the Klamath River at Orleans experienced median daily maximum water temperatures between 12.5 °C and 21.8 °C (USGS Station 11523000). Klamath River is accessible to Green Sturgeon along the 80 km downstream of Ishi Pishi Falls near the confluence of the Salmon River. Water temperatures along the Rogue River are less modified down-stream of William L. Jess Dam. During May and June from 1960 to 2012, the Rogue River at Agness experienced median daily maximum water temperatures between 13.1 °C and 21.0 °C (USGS Station 14372300). Green Sturgeon can access the lower 120 kilometers of the Rogue River below Raine Falls. In the Sacramento River during April through July, the water temperatures downstream of Keswick dam are cooler due to controlled releases (Figure 1). At Bend Bridge, median daily maximum temperatures between 1974 and 2012 ranged between 13.1 °C and 14.4 °C (USGS Station 11377100). Green Sturgeon larvae were collected each year in 2002 -2014. During the collection periods, the temperatures ranged between 12.8 °C and 16.1 °C with an average of 14.4 °C (Poytress et al. 2014). The cooler water of the Sacramento River led to concern that reduced water temperatures were negatively affecting growth and survival of larval and juvenile Green Sturgeon.

Another factor altering habitat available to Green Sturgeon was Red Bluff Diversion dam constructed across the Sacramento River in 1964. The dam contains 11 gates that divert water into an irrigation canal and when closed, pose a complete barrier to fish migrating upstream of the dam. From 1964 to 2011, the dam was operated in a manner that hindered the spawning

migrations of Green Sturgeon (Heublein et al. 2008). In 2011, water pumps were installed to replace the mechanical gates. The dam now is operated with the gates open year round and poses no barrier to fish migration. Green Sturgeon now have year around access to habitat upstream of Red Bluff Diversion Dam, below Shasta and Keswick Dams. Mora et al. (2009) found that this region of the Sacramento River is similar to the rivers occupied by the NDPS, suggesting that the historic distribution of Green Sturgeon extended much further upstream in the Sacramento River than currently accessible. Thus, since the construction of Shasta Dam, Green Sturgeon have experienced temporally shifting and highly altered spawning habitat. It is possible that flow and temperature regulation in the Sacramento River, combined with shifting historic habitat fragmentation may still constrain the ability of Green Sturgeon to seek and utilize higher quality spawning habitat.

In general, larval and juvenile Green Sturgeon display faster growth rates at higher water temperatures. Mayfield and Cech (2004) examined the growth of juveniles aged 144 days post hatch at three temperature regimes during a 33 day period and found an increased rate of growth between 11°C and 15°C, yet no difference between 15°C and 19°C. In larval Green Sturgeon, an increase in growth was exhibited as temperatures increased from 19°C to 24°C (Allen et al. 2006). Similarly, the upper limit of thermal optima for Green Sturgeon embryos was found to be between 17°C and 18°C, with deformities occurring at the lower limit of 11 °C (Van Eenennaam et al. 2005). The temperatures experienced in the Sacramento River are within a range of 11-15°C, and this likely limits Green Sturgeon growth.

In this study, we evaluate tradeoffs between various water management scenarios in the Sacramento River through mechanistic individual based models representing Green Sturgeon early life history. These models track growth, migration and survival of individual sturgeon as they experience varying rates of flow, water temperatures and turbidities after emerging from spawning and hatching locations (Poytress et al. 2013, Goto et al. 2015). We first compare four water management scenarios to evaluate how they differ with regard to survival and growth of larval and juvenile Green Sturgeon, using historical records of discharge, water temperatures and turbidity. We then draw upon 25 years of modeled temperature data to determine how growth and survival varied in the past. Finally, we determine how habitat fragmentation and temperature regulation has impacted the temporal and spatial distribution of Green Sturgeon spawning events.

## **<A>Methods:**

### **<B>Four Scenario Model Structure**

We developed an individual based model that tracks the age (days), length (mm), location (rkm) and mortality of juvenile Green Sturgeon over a 45 day period using the program R (R Development Core Team 2015). For each day, the model first determines the distance downstream each individual migrates and then references water temperature at that location based on a simple assumption of a linearly warming river. The model then updates the location of each individual, calculates the growth increment at that temperature and then updates the length of the individual. Finally, the model determines if each individual survives during the time period based on two functions; 1) a length-based mortality function and a turbidity effect on predation, where higher turbidity reduces the mortality rate due to predation and 2) a temperature

based mortality function. To evaluate their relative contribution to survival and growth, we varied the following: 1) temperature structure of the simulated environment, 2) migration rate of individuals, and 3) turbidity, in order to represent four typical management scenarios.

We simulated migration, growth, and mortality of 10,000 individuals over the course of 45 days. Parameters are described in more detail in the section below. The juveniles were initiated at a single confirmed spawning location (Poytress et al. 2013), from which they did not migrate for the first 10 days as observed by Kynard et al. (2005). Individuals then migrated downstream at the specified speed until day 21. After day 21 the fish held in place with a slight downstream bias (Kynard et al. 2005). After the daily movement was implemented, individuals were then exposed to the river temperature at their new location and experienced one day of growth. The final step of each daily update was to determine the mortality of each individual. The instantaneous daily mortality rate was calculated from the product of size-based mortality and a turbidity effect that reduces mortality (Goto et al. 2015). A random number was then drawn from a uniform random variable ranging 0-1. If the number drawn was less than the instantaneous daily mortality rate, the individual was considered deceased and was no longer included in the model.

We evaluated four scenarios that differed by two levels of flow and two temperature regimes (Figure 2). Flow volume, which correlates with water velocity, served to influence migration rate and turbidity while temperature influenced growth rate and mortality. Mortality was also influenced by the size of the individual. Conceptually, the low flow and high temperature quadrant of Figure 2 represents how the Sacramento River would function during Green Sturgeons spawning in the absence of the Shasta-Keswick infrastructure and is similar to the

Shasta Inflows pattern in Figure 1. The high flow, low temperature quadrant represents the realized function of the Sacramento River with the Shasta-Keswick infrastructure and is similar to the Keswick Outflows pattern for May and June in Figure 1.

<C>Model Inputs:

<D>Water Temperature:

Water temperature increased linearly with distance downstream to simulate a pattern of the river warming after release from Keswick and traveling through the relatively warm California Central Valley in May and June (Figure 3). The low temperature regime spanned 11-14°C. The high temperature spanned 14-17°C.

<D>Migration rate:

Movement was modeled as a normal random variable with mean equal to the migration rate on days 10-21 (Fast: .15m/s or 6.48km/day; Slow: .075 m/s or 3.24 km/day ) and 0.1 km/day on days 21 onward all with variance equal to 0.1. These downstream migration rates were arbitrarily selected because no studies of migration speeds have been performed for juvenile Green Sturgeon. Our estimates were based upon the migration and diel behavior experiments of Kynard et al. (2005) and by characteristics of larval Green Sturgeon capture locations in Poytress et al. (2014). Kynard et al (2005) found that during days 0-14, juveniles were completely benthic and larvae aged 0-10 days post hatch showed no migration and were under cover. Nocturnal migration began at days 14-18 days post hatch generally lasting 12 days. Kynard et al. (2005) describes the proportion of up- and downstream passes in a circular swimming apparatus by groups of larval and juvenile Green Sturgeon aged between 0-50 days post hatch then again at

56, 80, 110 and 155 days post hatch. In the Sacramento River, D-net sampling of larval and juvenile Green Sturgeon occurred in water speeds of .3-1.5m/s (Poytress et al. 2013). These velocities are greater than the values that we specify in the model. However, we assume that juvenile Green Sturgeon can seek water velocities consistent with their migration behavior. We assume they will utilize greater water velocities when migrating and when exhibiting holding behavior they will seek reduced or zero water velocities.

We started all individuals at river-kilometer 409, near the confluence with Paynes Creek. This location was selected to represent a known occupied location in the currently accessible region of the Sacramento River. This location is commonly occupied with by a large number of adult sturgeon during the spawning season, as indicated by DIDSON abundance estimates between 2010-2015 (Chapter 2).

#### <D>Growth Rate

Growth rates were a function of water temperature (Figure 4). Green sturgeon growth rates were taken from growth experiments (unpublished data, Nann Fangue). Juvenile Green Sturgeon were exposed to temperature treatments of 11, 13, 16, and 19 °C for 45 days at 25% and 100% food rations. Growth in fork length (mm) and mass (g) was measured at days 21 and 45. Our growth curves were taken from the 100% ration treatments. We fit a second order polynomial to the growth data to extrapolate growth should river temperatures exceed the interval 11-19 °C (Figure 4a and b). The equations fit to the 1-21 day interval is as follows:

$$\text{Length} = -0.0029x^2 + 0.1004x - 0.5731 \quad (R^2 = .99)$$

where x is the temperature in degrees Celsius.



$$\text{Mass} = -0.0045x^2 + 0.1529x - 0.9697 (R^2=.99).$$

The equation fit to the 21-45 day interval is

$$\text{Length} = -0.0027x^2 + 0.1013x - 0.7458 (R^2= .95)$$

$$\text{Mass} = -0.0097x^2 + 0.3677x - 2.8357 (R^2=.93)$$

<D>Survival:

Goto (2015) found that larval and juvenile mortality of Shovelnose Sturgeon (*Scaphirhynchus platyrhynchus*) occurred through three processes: high temperature, predation, and starvation. We included only predation and extreme temperatures as a factors influencing mortality as we lack information describing the dietary requirements of juvenile Green Sturgeon. Total mortality from these two sources was assumed to occur at an annual rate of 7% and was allocated evenly between these two sources of mortality (Deng et al. 2002, Beamesderfer and Simpson 2007). Predation-based mortality was assumed to be a function of size (Figure 5) and was parameterized from Goto *et al.* (2015).

Predation-based mortality was also impacted by turbidity level and acted as a scalar of mortality rate (Goto et al. 2015) [Figure 6]. Increased turbidity was found to reduce predation rates of White Sturgeon (*Acipenser transmontanus*) larvae in experimental trials (Gadomski and Parsley 2005). Low turbidity was assumed to be 10 Nephelometric Turbidity Units (NTU's) and high turbidity was assumed to be 100 NTU's, values within the range exhibited by USGS and CDEC turbidity monitoring stations throughout the study area.

The temperature-based component of mortality was adapted from research on Green Sturgeon by Van Eenennaam *et al.* (2005: Figure 1). We fit a second order polynomial to temperature-based mortality to extrapolate should the river temperatures exceed the interval 11 – 26 °C (Figure 8).

The daily temperature-based mortality function is as follows:

$$(m) = 0.0091x^2 - 0.2796x + 2.1735 (R^2=.98)$$

We analyzed results of the four scenarios using a two-way ANOVA to evaluate the effects of flow volume and thus migration speed, temperature and their interaction on the produced biomass of the four scenarios. All statistical tests were run using the base package of the program R.

### **<B>25 Year Hind Cast of Sacramento River Temperatures**

The NOAA Southwest Fisheries Science Center has developed a model that estimates Sacramento River water temperatures at 15 minute intervals within 2km reaches, with .25 °C error (Pike et al. 2013). This model produces 72 hour water temperature forecasts contingent upon Shasta-Keswick operations. Further development of the model has since incorporated 25 year hind-casts of water temperature and flow volumes. Collectively, this model provides fine scale information describing the temperatures that would be experienced by juvenile Green Sturgeon during their incubation and downstream migration. We utilized this 25 year time series of modeled Sacramento River water temperatures to visualize if any discernible variations in growth and survival were apparent. As there are no indices of juvenile Green Sturgeon

recruitment and survival, we were unable to compare our model to any time series of these indicators.

We utilized recoded turbidity measures from the Red Bluff CDEC station for all days of the simulation, the same size based predation relationship, and the same size and temperature based mortality relationships as the Four Scenario model. We set all individuals to begin migration on the 120<sup>th</sup> day of the year (April 20<sup>th</sup>) and the model tracked the first 45 days of the individuals. Migration rate was selected to be the average of the fast and slow rates implemented in the Four Scenario model (4.86 km/day). We ran the model for these years and not the full 25 year period because the turbidity data were limited to the years 1999 through 2014. To reflect the historical extent of available spawning habitat, in this application of the model, individuals were started below Red Bluff Diversion Dam at a known spawning location at river kilometer 391 (Poytress et al. 2011, 2012, 2013).

### **<B>Comparison of Detected Spawning and Available Habitat**

We extended the model to test the hypothesis that habitat fragmentation has decoupled Green Sturgeon from their ability to select the locations that maximize the growth and survival of their offspring. We calculated the spatial and temporal average of the 25 year hind-cast of river temperature. Thus, for each day of the year, and at each river location in the study area, we calculated the 25 year average water temperature location for that entry. This created a map of the average structure of water temperature in time and space. Next, we built a map of ‘productivity’ of every possible location x date possible because we have the ability to estimate the expected produced biomass of cohorts beginning migration at any combination of time and

location and a map of the average thermal environment they will experience during their outmigration. In all models, productivity was calculated by summing the masses in grams of all individuals surviving the simulation.

We incorporated two additional pieces of information into our model. First, we determined the emergence time and location of 60 spawning events from the locations described in Poytress et al. (2009, 2010, 2011, 2012, 2013). To convert spawn dates from the Fish and Wildlife surveys to hatch dates, we assumed that the mean time from fertilization to hatch was 144 hours (Van Eenennaam et al. 2005, Poytress et al. 2013). However, time to mid-hatch is a function of water temperature with slower incubation occurring at lower temperatures and quicker incubation occurring with warmer temperatures (Van Eenennaam et al. 2005). Second, we summarized the 50<sup>th</sup> percentile entry and exit dates into and out of the study area for 61 complete spawning migration of acoustically tagged Green Sturgeon.

We next summed the productivity of each day of the year along the course of the river to test the hypothesis that Green Sturgeon are maximizing their productivity in time. This vector of temporal productivity indicates the day(s) of the year when productivity of emerging offspring would be the greatest. We used a one-way ANOVA and pair-wise Welch Two Sample t-tests to compare the productivity of three date samples. This involved: 1) determining the dates of detected spawning events (N=60) by USFW egg mat sampling during the years 2008 - 2012 and sampling those dates from the vector of daily productivity; 2) sampling the 60 dates from the vector of daily productivity that indicated the greatest values; and 3) sampling 60 random dates

within the 50<sup>th</sup> percentile entry and exit time interval to represent a random sample of dates when Green Sturgeon were occupying their spawning habitat and could potentially spawn.

We summed the productivity of each location within the sample space for all days during the year within the productivity map to test the hypothesis that Green Sturgeon are maximizing their productivity in space. This vector of spatial productivity within the study area indicates the locations where the productivity of emerging offspring would be the greatest. We used a one-way ANOVA and pair-wise Welch Two Sample t-tests to compare the productivity of the three spatial samples including: 1) determining all of the locations of detected spawning events (N=7) by USFW egg mat sampling during the year of 2008-2012 and extracting their values from the vector of spatial productivity (Poytress et al. 2009, 2010, 2011, 2012, 2013)<sup>1</sup>; 2) sampling the 7 locations from the spatial productivity vector that indicated the greatest productivity; 3) selecting seven random values from the vector of spatial productivity to represent a random set of locations within the study area.

We evaluated the hypothesis that Green Sturgeon are maximizing their productivity in time and space. To do this, we used a one-way ANOVA and pair-wise Welch Two Sample t-tests to compare the productivity of three samples, as follows: 1) sampling the 60 date time combinations with the greatest productivity values from our productivity map 2) sampling the calculated productivity values from the 60 detected spawning events; 3) sampling the expected productivity from 60 random points within the time and space interval containing the entire study

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<sup>1</sup> Sampling for this group of detected spawning locations spanned the entire range of detected sturgeon occupancy from Chapter 2 of this dissertation.

area and the 50<sup>th</sup> percentile entry and exit time interval. These three samples represent the maximum possible productivity, the realized productivity, and a random sample of productivity respectively. This version of the model assumes no spatial structure in food, predation or turbidity.

## <A>Results:

### <B>Four Scenario Model

We plotted the size, location and the number of surviving individuals from each scenario (Figure 6). The highest survivorship occurred in scenario D, followed in order by scenario B, A, and C. The largest individuals were the result of scenario B, followed in order by D, A and C. As there was only one variable controlling migration rate, flow volume, scenarios A and B tied with the furthest downstream migration and scenarios C and D tied with the shortest migration distance.

Scenarios B and D produced the most beneficial results to Green Sturgeon growth and survival. These two scenarios were comprised of ‘high’ water temperatures and differed by migration rate and turbidity. This resulted in differing survivorship stemming from size and turbidity based mortality. The two least advantageous scenarios to Green Sturgeon growth and survival (A and C) were the result of ‘low’ water temperatures and also differed by migration rate and turbidity.

A two-way ANOVA showed that there was a significant difference in means of accumulated mass between the four treatments (Table 1). Flow had a significant effect on accumulated biomass ( $F(1,4146) = 1816.6, p < 2.2e-16$ ) as did Temperature ( $F(1,4146) = 1942.8, p < 2.2e-16$ ) and the interaction of Flow \* Temperature ( $F(1,4146) = 23.5, p = 1.3e-06$ ). A survey of the model effect sizes (Factor-Intersect) indicates that the largest effect on accumulated mass was from

temperature, while the interaction of flow\*temperature was second and the least effect was flow alone.

### **<B>25 Year Hind Cast of Sacramento River Temperatures**

We plotted the size, mass, and survival of individuals, and total biomass production of each year between 1999 and 2014. As all model runs utilized the same migration speed, there was no difference in distance traveled and that result was omitted from Figure 9. There was no apparent trend in productivity as total produced biomass ranged between 160,000 and 200,000 grams per year. The years 2011 and 2010 stood out as apparently low productivity years while the most recent period between 2012 and 2014 displayed the greatest productivity in biomass, size and mass of individuals. The years 2009-1999 were all very similar in results. We were unable to verify the results of this hindcast with comparisons of other measures of productivity as there are no historical time series of Green Sturgeon abundance.

### **<B>Comparison of detected spawning and available habitat**

We calculated the 50<sup>th</sup> percentile entry date to occur on April 13<sup>th</sup> of each year. The 50<sup>th</sup> percentile exit date occurs on November 29<sup>th</sup> of each year. The 60 detected spawning events are shown in Table 2.

A plot of summed productivity of each day shows a peak in productivity on day 168, June 17 (Figure 11). The 60 days of greatest productivity spanned the period day 134 to 199 (May 14<sup>th</sup> to July 18<sup>th</sup>). A one-way ANOVA showed a significant difference between the three temporal samples of productivity  $F(2,177) = 26.55, p < .05$ . Pair-wise comparisons using Welch Two Sample t-tests were significantly different between all samples at the  $p < .05$  level indicating that

Green Sturgeon are not spawning during the days that would maximize the growth and survival of their offspring. These results also indicate that Green Sturgeon are selecting dates to spawn that improve the survival and growth of their offspring when compared to a random selection of dates (Figure 12).

A plot of summed productivity of each location shows a peak in productivity 51 miles downstream of Keswick Dam (River Mile 251) just downstream of the confluence of Payne's Creek. (Figure 13). This fact agrees with the distribution data gathered in Chapter 2 of this thesis as that region consistently sets the record for greatest sturgeon in one location. The 8 locations of greatest productivity spanned the locations 49 – 55 miles downstream of Keswick, (River Miles 251 to 245). A one-way ANOVA showed no significant difference between the three spatial samples of productivity  $F(2, 18) = 1.993$ ,  $p=.165$ . Pair-wise comparisons using Welch Two Sample t-tests also were not significantly different between all samples at the  $p<.05$  level. These results indicate that Green Sturgeon are not selecting locations to spawn that improve the survival and growth of their offspring when compared to a random selection of spawning sites in the study area (Figure 14).

Our map of expected productivity displays the 60 greatest values between 66 and 103 miles downstream of Keswick during the dates of June 29<sup>th</sup> (the 180<sup>th</sup> day of the year) and August 10<sup>th</sup> (the 222<sup>nd</sup> day of the year) (Figure 15). A one-way ANOVA of the three time-space samples shows a significant difference in productivity between the three samples ( $F(2, 177) = 85.17$ ,  $p<.05$ ). Pair-wise comparisons using Welch Two Sample t-tests were significantly different



between all samples at the  $p < .05$  level. This indicates that Green Sturgeon are not spawning during the days and locations that would maximize the growth and survival of their offspring. These results also indicate that Green Sturgeon are selecting instances to spawn that improve the survival and growth of their offspring when compared to a random selection of instances (Figure 16).

### **<A>Discussion:**

The results of individual based models suggest that water temperature and its effect on growth had the greatest influence on growth and survival of juvenile Green Sturgeon. Other aspects such as size-based and turbidity-based predation and migration speed had less of an effect on the growth and survival of individuals. Migration speed and thus, river flow, in this model generally served as a proxy for the rate that the individuals increased their temperatures, as the river generally warmed as it travels downstream in the warm California Central Valley summers.

The current situation experienced by juvenile Green Sturgeon in the Sacramento River is most similar to scenario C (low water temperatures and low flows). Recall, scenario C performed the worst by measures of total biomass produced, and total growth, accumulated mass, and survival of individuals. Thus, it appears, many alternative management scenarios may be beneficial to the growth and survival of juvenile Green Sturgeon, particularly any scenario which warms the river.

The results of our study show that thermal regime of the Sacramento River is within a tolerable, yet sub-optimal range of juvenile Green Sturgeon. The growth trials found no significant effect of temperature on survival within the range of 11-18 °C. This is consistent with the findings of

Van Eenennaam et al. (2005; Figure 1). This trend is also visible in Figure 8 of this chapter. At extreme temperatures, Van Eenennaam et al. (2005) did find an effect on survival by water temperatures. Those authors found that 17-18 °C may be the upper limit to thermal optima and deformities occurred at lower water temperature. The growth trials all displayed peak growth rates at 16° C and growth rates were slightly less in trials at 18°C. This indicates a narrow range of optimal temperatures for the growth and survival of juvenile Green Sturgeon. This is especially interesting because the river temperatures experienced by NDPS are often in this range. In contrast, the water temperatures are often lower within the reaches of Sacramento River during the months of peak spawning by Green Sturgeon (Figure 1). Conversely, a warmer temperature regime may be tolerable, should tradeoffs between the cooler, temperature regime prescribed for Central Valley salmonids be found with Green Sturgeon. Our study provides the framework to begin asking just how much Green Sturgeon productivity would be lost should an alternative water management scenario be prescribed.

Our results also suggest that Green Sturgeon are now able to access spawning habitat that maximizes the growth and survival of their offspring. However, they are not necessarily selecting to spawn at the specific combinations of time and space that maximize growth and survival. The results of the temporal and spatial time slice display that Green Sturgeon have access to the region of the river with the greatest average productivity and are occupying the study area during the times of the year with the greatest average productivity. The temporal and spatial time slices as well as from the productivity map show that Green Sturgeon display productivity much greater than the random samples yet not as great as those samples containing the highest values. We hypothesize that this discrepancy is likely due to one or all of three

factors: 1) altered environmental cues result in Green Sturgeon selecting spawning sites that deviate from optimal; 2) the recorded spawning events were from too limited a sample size to accurately represent the true pattern of Green Sturgeon spawning; 3) additional factors exist that cue Green Sturgeon to spawn, such as substrate composition or the presence of con-specifics. Thus, the re-operation of Red Bluff Diversion Dam removed a barrier to apparently high productive spawning habitat, which Green Sturgeon are utilizing to their benefit, but not optimally.

Care should be taken when applying the results of this model to determine water releases into the Sacramento River. Flow volume is a variable in all models however it served to impact migration rate and turbidity only. It was assumed that increased flow volume would increase water velocities and thus the capacity for juvenile Green Sturgeon to migrate downstream. It was also assumed that increased water velocities would increase sheer stress along the riverbed and thus entrain sediment and increase turbidity. Thus, any water management actions should address these two confounding variables directly since they correlate with flow volume.

Food availability is an important component not included in this model. Growth experiments performed by the University of California at Davis included trials at 100% and 25% food rations and the growth curves implemented in this model were from the 100% ration trials. Those experiments showed a reduced growth due to food limitation, which likely occurs in wild populations. In the summer of 2015, the United States Fish and Wildlife Service performed targeted sampling for Green Sturgeon juveniles and was able to capture individuals spanning 73-344mm. (Josh Gruber, U.S. Fish and Wildlife, personal communication). Their sampling

occurred in a 20 km reach centered in Red Bluff, CA (Rkm 390) and their samples generally consisted of two concurrent cohorts differing in size. The functions of our model suggest that the difference in size between these two groups is either the result of reduced food intake by the smaller group or the temporal separation of spawning by adults. To this disparity, we suggest a study be carried out that identifies the specific prey items of juvenile green sturgeon followed by a survey of the Sacramento River to determine how the availability of these prey items vary in time and space.

While temperature had the largest effect on survival and growth, migration rate still performs an important role in the early life history stage of Green Sturgeon. A literature search failed to identify previous studies describing the downstream migration of any sturgeon species. The values selected in this model were reasonable placeholders to use while developing the model and they seemed to be reasonable in light of the actual growth trials and the U.S. Fish and Wildlife samples from 2015. We recommend continued development of the U.S. Fish and Wildlife sampling to include marking of individuals and the initiation of a second sampling station to identify the rate at which juveniles migrate downstream. It is important to determine if there is a relationship between size and migration rate.

Finally, these models only analyze the first 45 days after emergence and do not account for what is happening outside of the study area or other seasonal trends occurring later in the life of the individuals. For instance there is very likely a seasonal and spatial trend in predation, turbidity and food availability that would influence the spawn date, survival and growth of juvenile green

sturgeon. These topics are better incorporated into a model describing the entire life cycle of SDPS Green Sturgeon.

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|           | Df   | Sum Sq | Mean Sq | F value | Pr(>F)      |
|-----------|------|--------|---------|---------|-------------|
| Flow      | 1    | 2353   | 2352.5  | 1816.6  | < 2e-16 *** |
| Temp      | 1    | 2516   | 2516.0  | 1942.8  | < 2e-16 *** |
| Flow:Temp | 1    | 30     | 30.4    | 23.5    | 1.3e-06 *** |
| Residuals | 4146 | 5369   | 1.3     |         |             |

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

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Coefficients:

|                         | Estimate | Std. Error | t value | Pr(> t )    |
|-------------------------|----------|------------|---------|-------------|
| (Intercept)             | 19.59596 | 0.02520    | 777.562 | < 2e-16 *** |
| FlowLowFlow             | -1.60875 | 0.03552    | -45.297 | < 2e-16 *** |
| TempLowTemp             | -7.36612 | 0.18878    | -39.021 | < 2e-16 *** |
| FlowLowFlow:TempLowTemp | -2.43396 | 0.50210    | -4.848  | 1.3e-06 *** |

---  
Signif. codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.138 on 4146 degrees of freedom  
Multiple R-squared: 0.4771, Adjusted R-squared: 0.4767  
F-statistic: 1261 on 3 and 4146 DF, p-value: < 2.2e-16

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Table 1: Results of two way ANOVA from the Four Scenario Model.

| RKm   | Spawn Date | Emergence Date |
|-------|------------|----------------|
| 424.5 | 4/30/2008  | 5/6/2008       |
| 424.5 | 5/3/2008   | 5/9/2008       |
| 377   | 5/8/2008   | 5/14/2008      |
| 377   | 5/9/2008   | 5/15/2008      |
| 377   | 5/12/2008  | 5/18/2008      |
| 377   | 5/15/2008  | 5/21/2008      |
| 377   | 5/17/2008  | 5/23/2008      |
| 377   | 6/5/2008   | 6/11/2008      |
| 377   | 6/7/2008   | 6/12/2008      |
| 377   | 6/9/2008   | 6/13/2008      |
| 424.5 | 6/10/2008  | 6/16/2008      |
| 391   | 6/19/2008  | 6/25/2008      |
| 377   | 7/4/2008   | 7/10/2008      |
| 424.5 | 4/2/2009   | 4/8/2009       |
| 424.5 | 4/3/2009   | 4/9/2009       |
| 424.5 | 4/5/2009   | 4/11/2009      |
| 424.5 | 4/21/2009  | 4/27/2009      |
| 424.5 | 4/22/2009  | 4/28/2009      |
| 377   | 4/23/2009  | 4/29/2009      |
| 377   | 5/10/2009  | 5/16/2009      |
| 377   | 5/12/2009  | 5/18/2009      |
| 377   | 5/25/2009  | 5/31/2009      |
| 377   | 5/26/2009  | 6/1/2009       |
| 407.5 | 5/26/2009  | 6/1/2009       |
| 377   | 5/28/2009  | 6/3/2009       |
| 377   | 6/4/2009   | 6/10/2009      |
| 377   | 6/5/2009   | 6/11/2009      |
| 377   | 6/12/2009  | 6/18/2009      |
| 377   | 6/13/2009  | 6/19/2009      |
| 377   | 6/14/2009  | 6/20/2009      |
| 377   | 6/20/2009  | 6/26/2009      |
| 391   | 6/26/2009  | 7/2/2009       |
| 424.5 | 5/4/2010   | 5/10/2010      |
| 424.5 | 5/5/2010   | 5/11/2010      |
| 424.5 | 5/6/2010   | 5/12/2010      |
| 424.5 | 5/8/2010   | 5/14/2010      |
| 426   | 5/8/2010   | 5/14/2010      |
| 424.5 | 5/17/2010  | 5/22/2010      |
| 424.5 | 5/18/2010  | 5/23/2010      |
| 424.5 | 5/19/2010  | 5/25/2010      |
| 424.5 | 5/20/2010  | 5/26/2010      |

|       |           |           |
|-------|-----------|-----------|
| 424.5 | 5/21/2010 | 5/27/2010 |
| 377   | 6/12/2010 | 6/18/2010 |
| 377   | 6/13/2010 | 6/19/2010 |
| 377   | 6/13/2010 | 6/19/2010 |
| 332.5 | 5/15/2011 | 5/21/2011 |
| 426   | 6/10/2011 | 6/16/2011 |
| 426   | 6/14/2011 | 6/20/2011 |
| 391   | 6/26/2011 | 7/1/2011  |
| 391   | 6/27/2009 | 7/3/2011  |
| 424.5 | 4/29/2012 | 5/3/2012  |
| 424.5 | 5/1/2012  | 5/7/2012  |
| 424.5 | 5/2/2012  | 5/8/2012  |
| 424.5 | 5/3/2012  | 5/9/2012  |
| 426   | 5/10/2012 | 5/16/2012 |
| 426   | 5/11/2012 | 5/17/2012 |
| 426   | 5/13/2012 | 5/19/2012 |
| 426   | 5/14/2012 | 5/20/2012 |
| 424.5 | 5/19/2012 | 5/25/2012 |
| 332.5 | 5/25/2012 | 5/31/2012 |

Table 2: Spawning and emergence dates of 60 detected spawning events detected by Poytress et al. (2009, 2010, 2011, 2012, 2013).

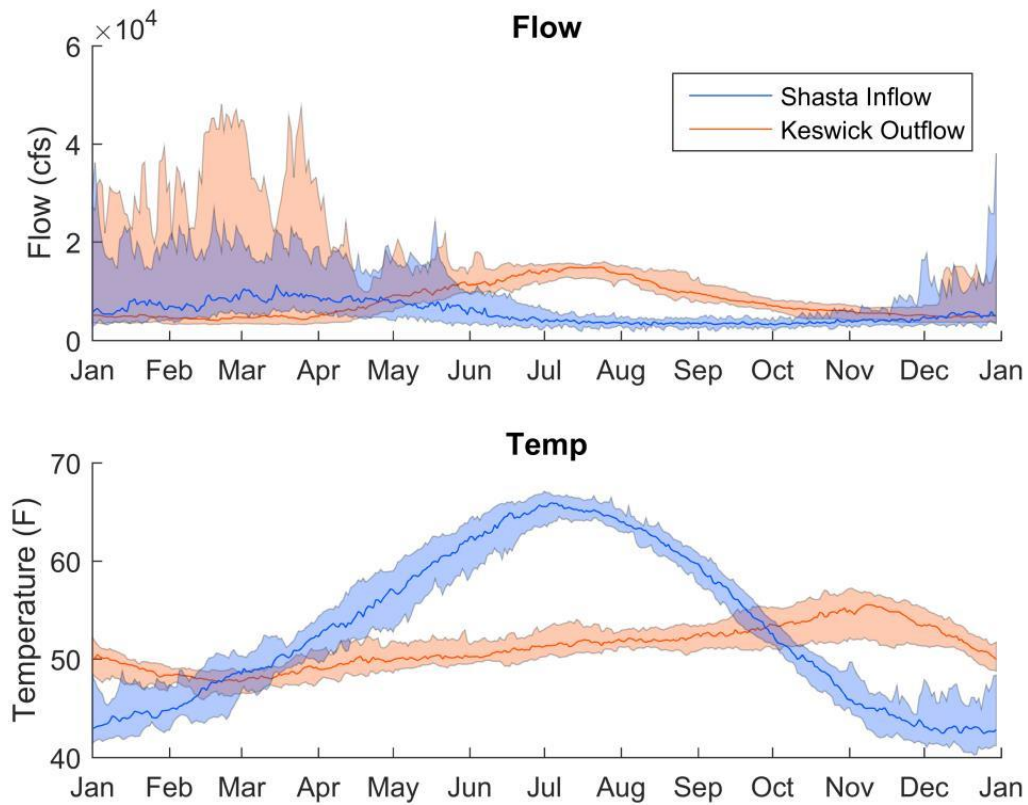


Figure 1: A comparison of Shasta Reservoir Inflows and releases from Keswick Reservoir. 25 years of Shasta inflow and Keswick outflow temperatures and flow volumes. The solid red and blue lines indicate the mean while the shading indicates the range. During the summer months, Sacramento River flow volumes are artificially increased while water temperatures are artificially reduced. Data and plot courtesy of Andrew Pike (NOAA-NMFS).

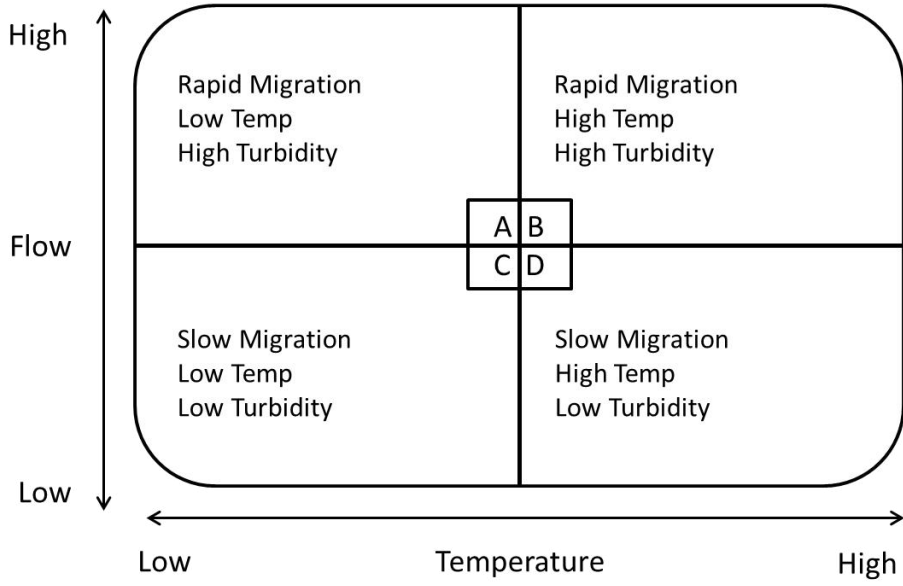


Figure 2: The Four Modeled Scenarios.

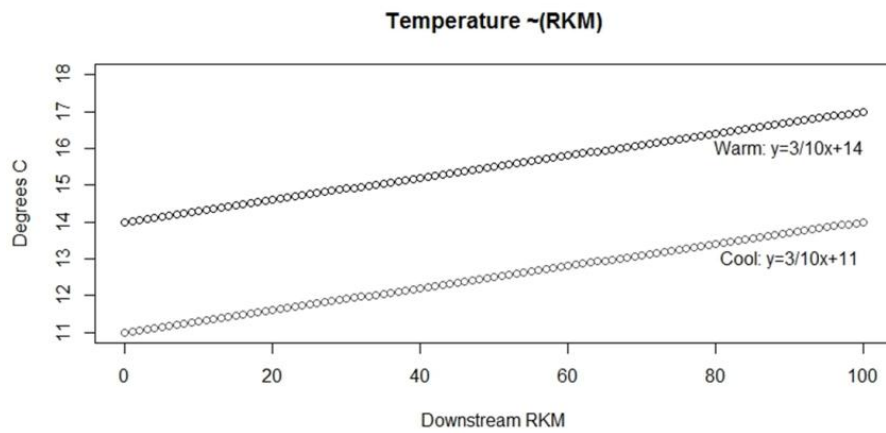
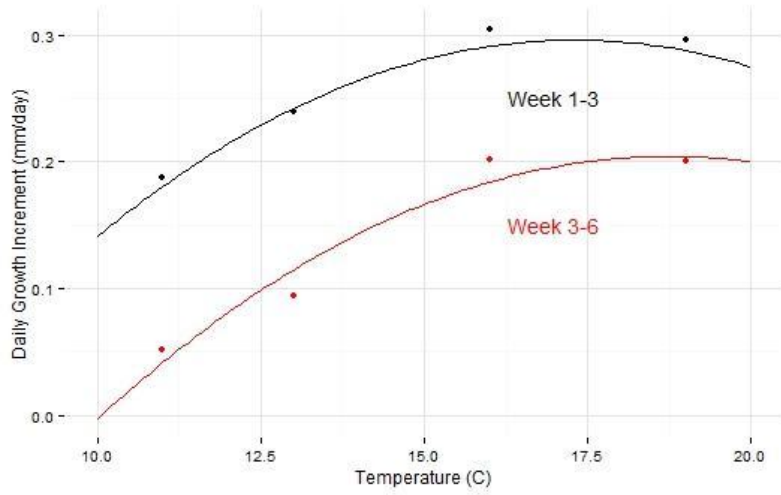
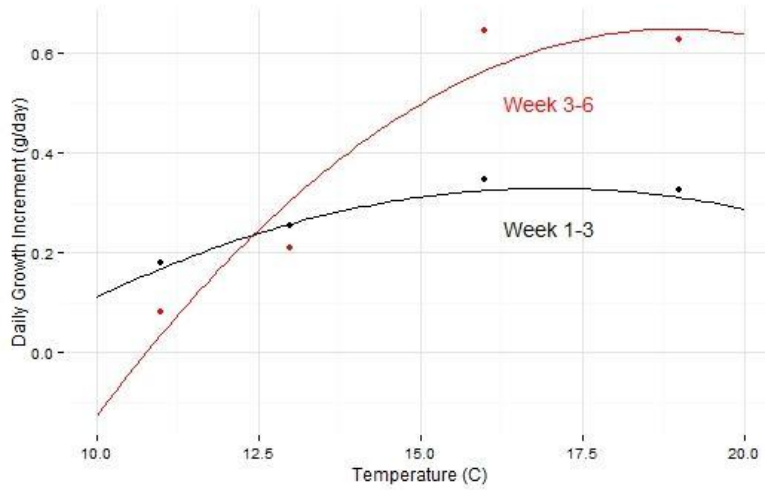


Figure 3: Assumed water temperature regimes in the four scenario model. Distance is downstream from Keswick Dam (Rkm 0).



a



b

Figure 4a and b: Results of the University of California at Davis growth trials by length (a; growth in mm/day) and weight (b; growth in g/day) during two different time periods.



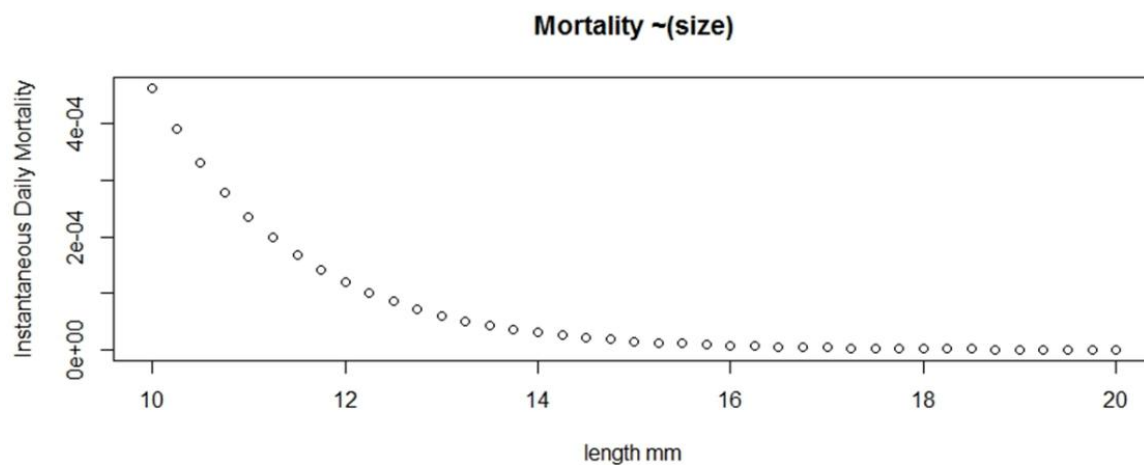


Figure 5: The size based mortality function used in all models.

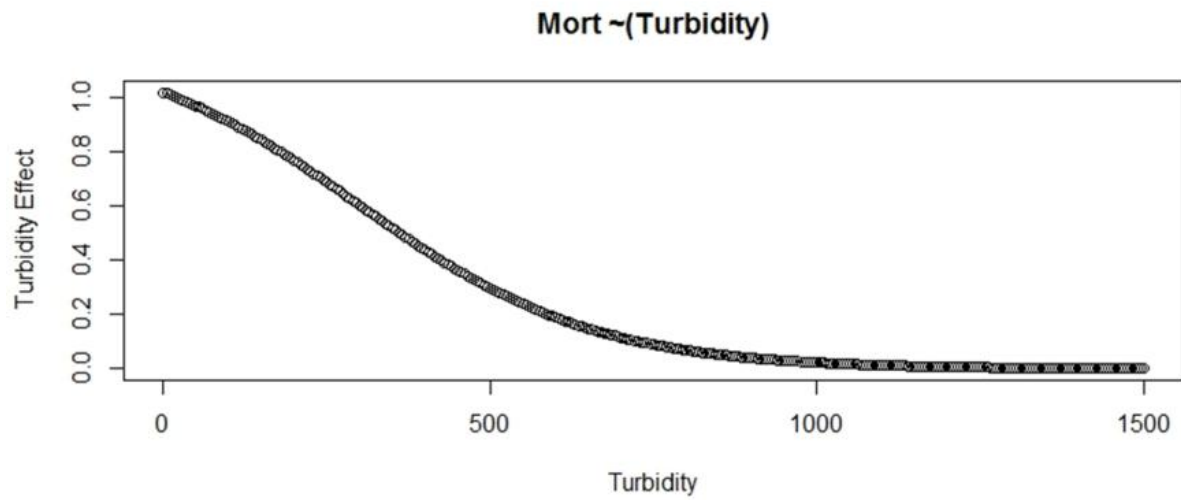


Figure 6: A plot of the ‘Turbidity Effect Scalar’. Here, predation based mortality rate decreases with increasing turbidity as the scalar moves towards zero at higher turbidity levels. Note that at lower turbidity levels, the scalar moves closer to one and reduces the ‘Turbidity Effect’ on predation.

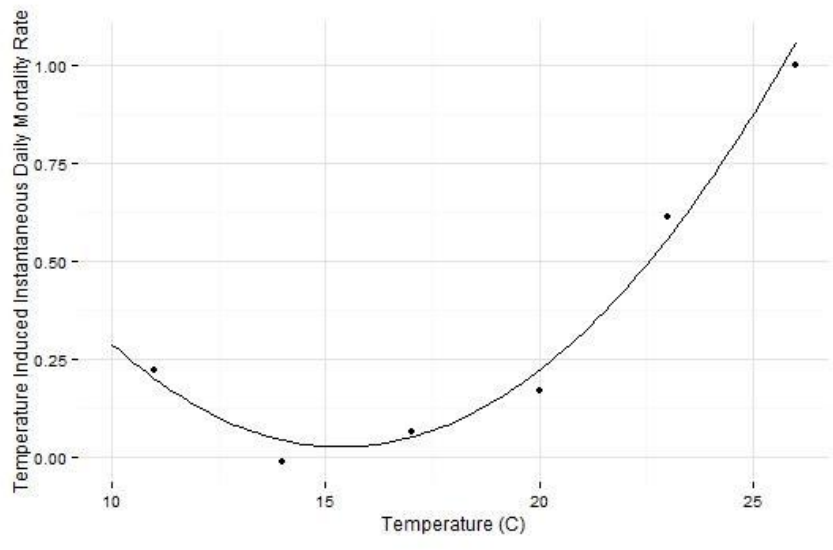


Figure 7: Plot of the temperature based mortality curve used in all models.

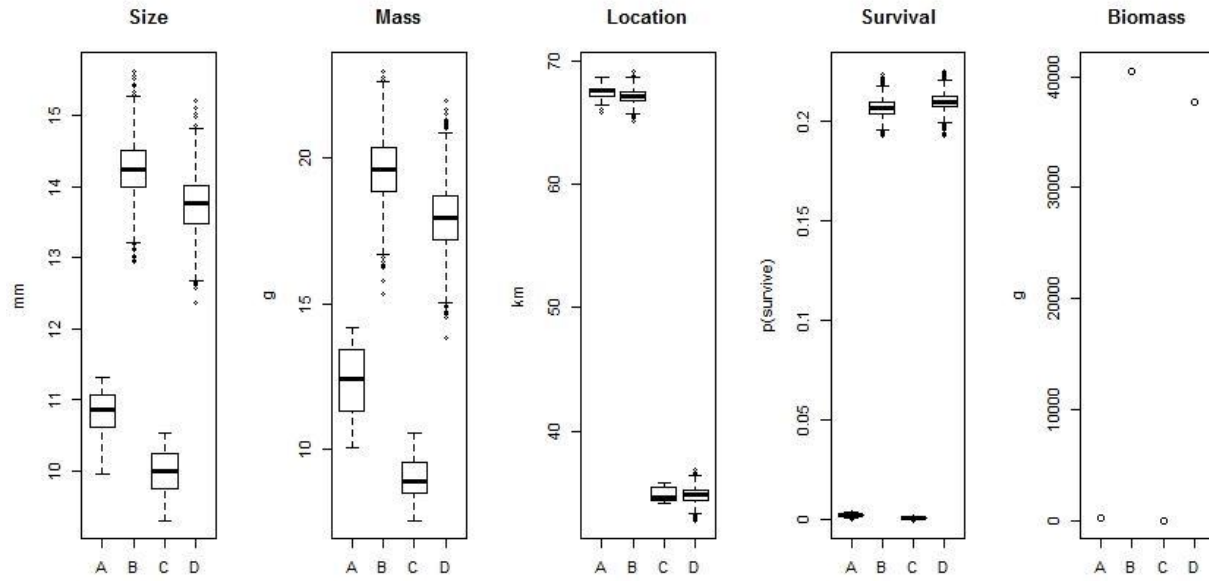


Figure 8: Results of the Four Scenario Model. Scenarios listed from left to right A,B,C,D.

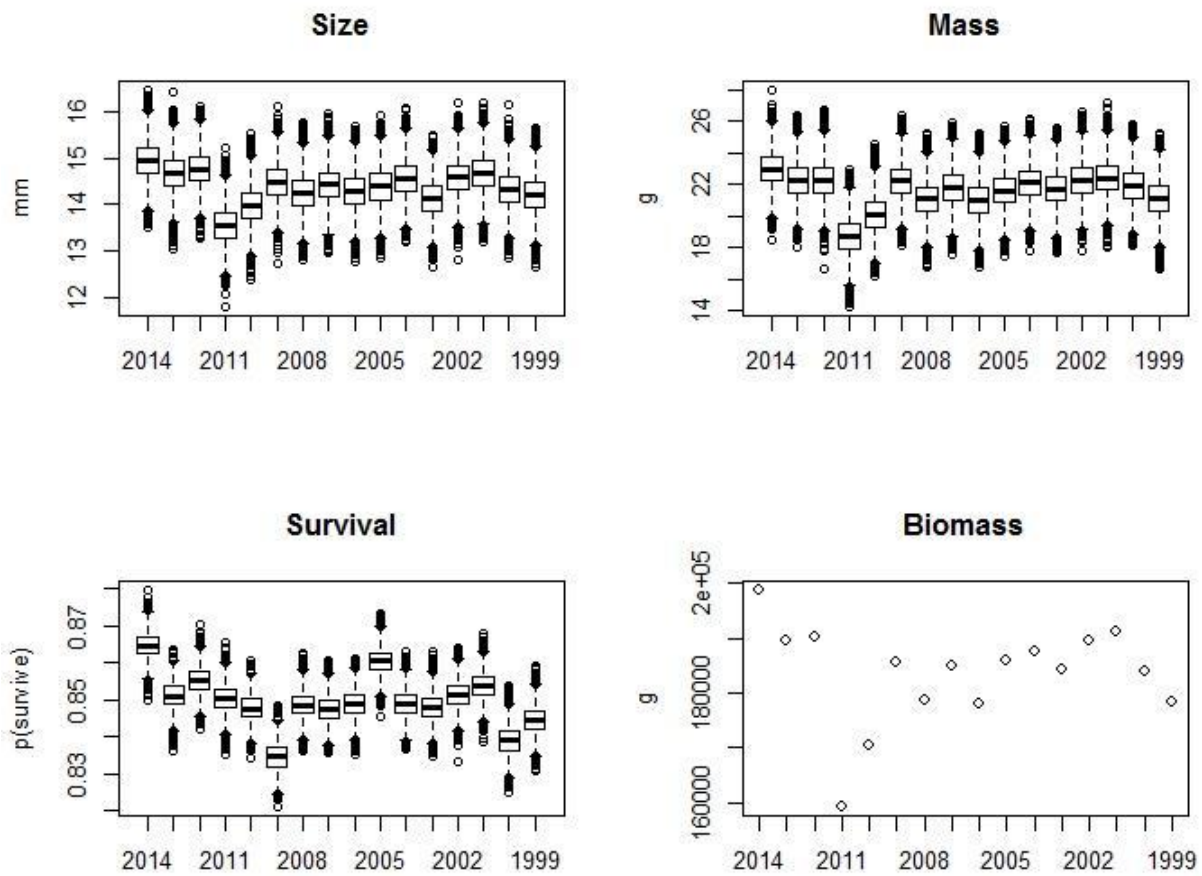


Figure 9: Estimated size, mass, survival, and biomass for each year of the 25 year hindcast model.

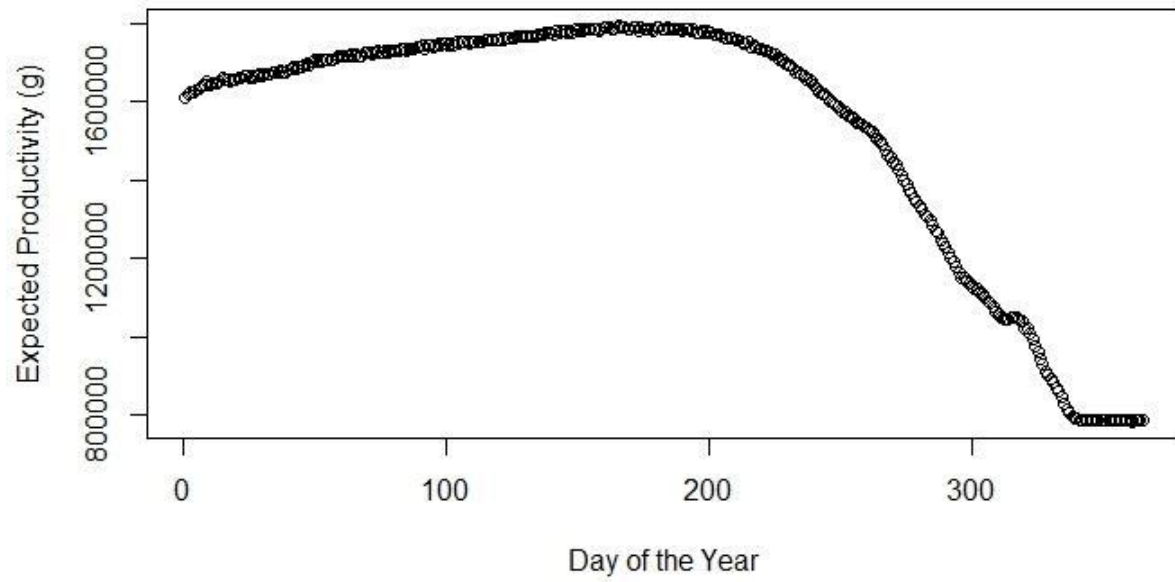


Figure 10: A plot of summed expected productivity per day. Productivity is lowest in the winter and peaks on day 168.

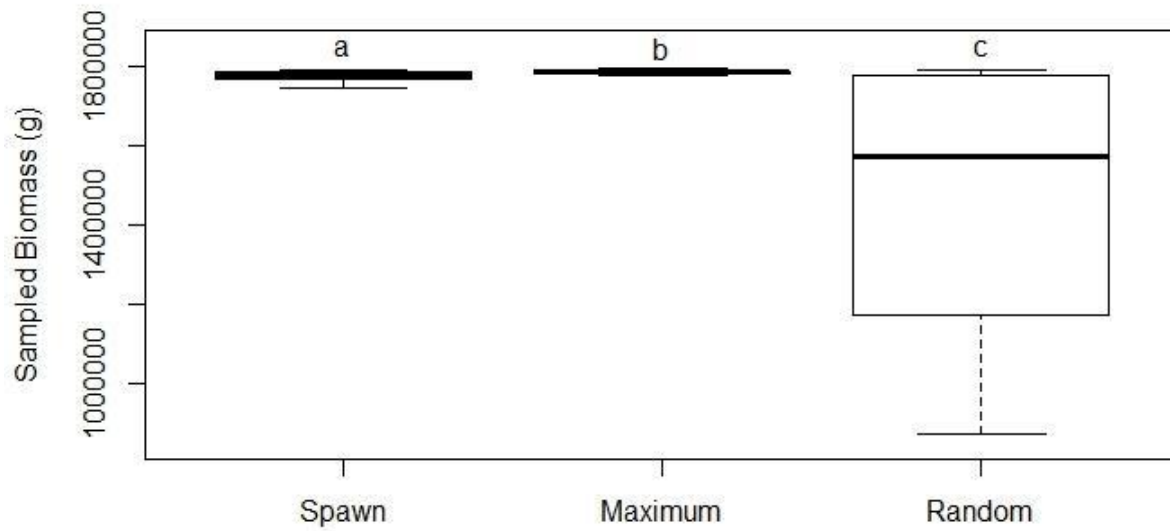


Figure11: Boxplot of three samples from the temporal productivity vector. Spawn is the sample from the 60 detected spawning events, Maximum is the sample of the 60 greatest values and Random is 60 random draws from the temporal productivity vector. Different lowercase letters indicate significant differences between samples.

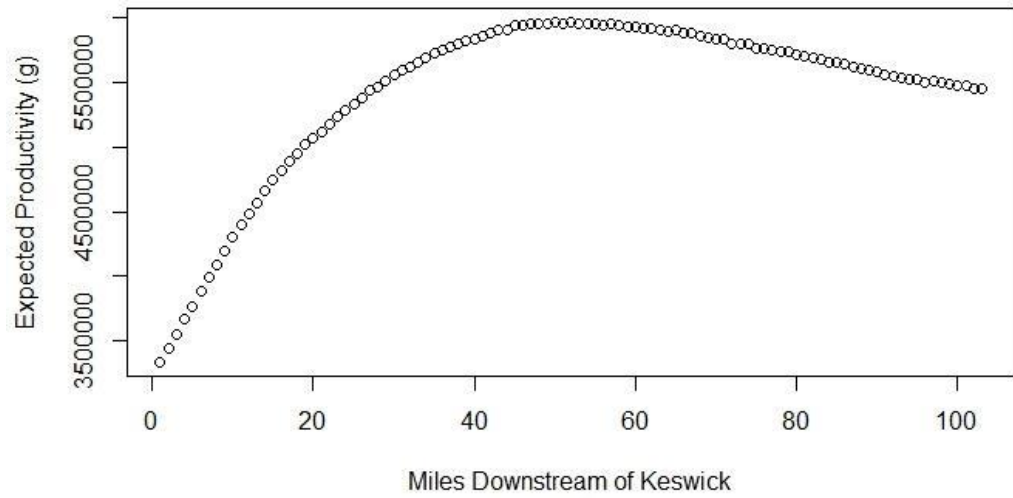


Figure 12: A plot of summed expected productivity. Productivity is lowest immediately below Keswick and increases downstream. Productivity decreases as the river warms farther downstream.



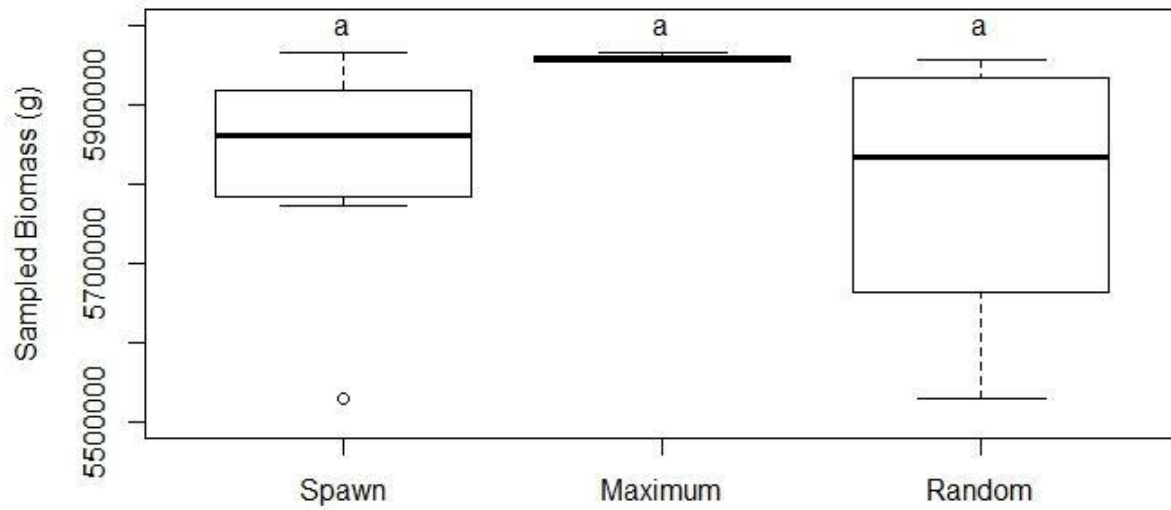


Figure 5: Boxplot of three samples from the spatial productivity vector. Spawn is the sample from the 8 detected spawning locations, Maximum is the sample of the 8 greatest values and Random is 8 random draws from the spatial productivity vector. Different lowercase letters indicate significant differences between samples.

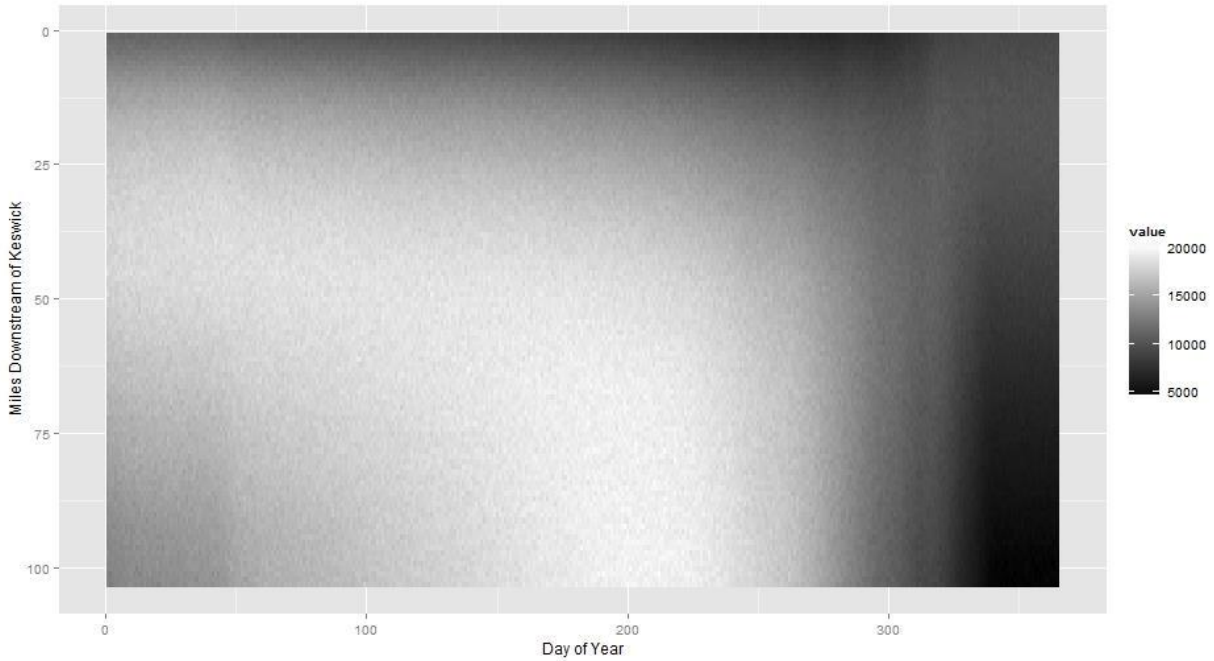


Figure 14: Productivity map of study area in grams of biomass. Each cell value represents the expected productivity of cohorts emerging and surviving downstream migration from each combination of date and location. A region of low productivity is shown near day 300 along the entire river as shown near the right side of the plot. A region of greatest productivity is shown near day 210 and between 75 and 100 miles downstream from Keswick.

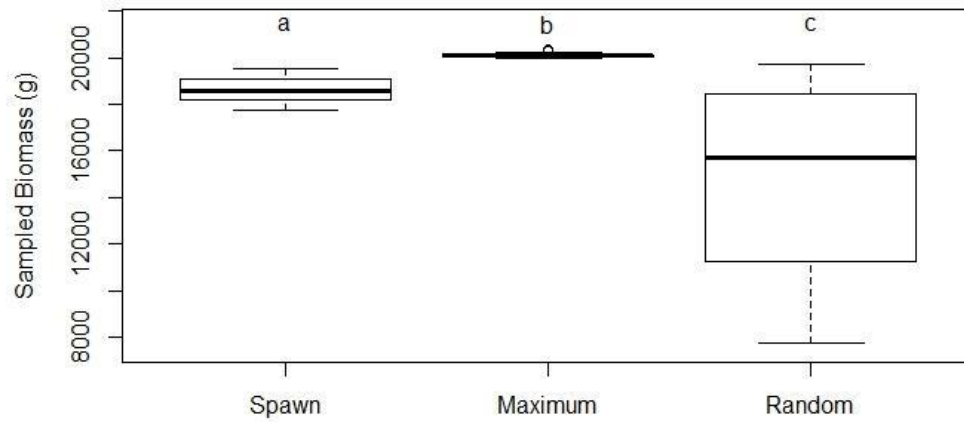


Figure 15: Boxplot of three samples from the productivity map. Spawn is the sample from the 60 detected spawning events, Maximum is the sample of the 60 greatest values and Random is 60 random draws from the productivity map of the study area and within the 50<sup>th</sup> percentile entry and exit dates. Different lowercase letters indicate significant differences between samples.